been identified with *Annalepis* by Wang & Lou (1990). In addition, it seems possible that the vertically compressed strobilar discs named *Isoetites* (*Lepacyclotes*) *circularis* (Emmons) by Brown (1958) may be generically equivalent (Bock, 1969), and possibly the material of Daugherty (1941: pl. 12, figs. 1, 2, but not pl. 15, figs. 1, 2). These specimens deserve fresh study.

If the North American material proves congeneric with *Annalepis*, it may be significant that there is a regional association with structurally preserved axes 1–2 cm wide described by Daugherty (1941) as *Chinlea* and *Osmundites walkeri* and referred to the lycopsids by Miller (1968). Other rare early Mesozoic stems such as *Grammaeophloios* (up to 3.5 cm wide) of Harris (1935) and the considerably larger *Ferganodendron* Dobruskina (1974) represent more substantial axes of the kind that might have been necessary to support *Annalepis/Lepacyclotes* sporophylls.

PLEUROMEIA

The "classic" subarborescent lycopsids of the Triassic, figured in almost every textbook on paleobotany, are those attributed to *Pleuromeia* (Fig. 1). This genus, often preserved spectacularly in permineralized form, is known from many mid-latitude Northern Hemisphere localities of early to middle Triassic age (see Mägdefrau, 1931; Neuburg, 1960; Dobruskina, 1974; Wang & Wang, 1982; but cf. Retallack, 1975, who includes the Southern Hemisphere genus *Cylostrobus* and other non-pleuromeian material). The plants ranged from 2–30 cm in height, i.e., distinctly herbaceous (Wang & Wang, 1982), to more typically 2–3 m. They were heterosporous but the strobili were monosporangiate, with rounded, partly sunken sporangia borne adaxially on sporophylls of a distinct broad ovate form unique to the genus. The sporophylls were crowded to give the strobilus an imbricate appearance. In situ spores were trilete and have been described by Neuburg (1960), Chaloner & Boureau (1967), and Yaroshenko (1975). Anatomical structure was studied by Snigirevskaya & Srebrodolskaya (1986). Srebrodolskaya (1988) showed that cambial activity at certain levels in the axis was lacking. This suggests an herbaceous to suffrutescent habit even for the larger species. Although the basal anchoring organ of the larger forms was four-lobed, like a highly reduced lepidodendralean rhizophore, that of the diminutive herbaceous (though fully fertile) forms is simply bulbous, with no apparent lobing.

As noted by Retallack (1975), rooted plants at Bernberg were almost certainly growing in freshwater, as were those described by Wang & Wang (1982). Evidence that some stands or species grew in, as opposed to being deposited in, brackish environments as claimed by Retallack (1975) is in need of critical reappraisal. The common environments of deposition that are preserved in the sedimentary record for most Mesozoic plants were coastal plain/deltaic or shallow marine. Monodominant assemblages may be locally or regionally derived, that is, of two distinct types. Although they may indicate actual growth in brackish environments such as marine embayments, discrimination of the exact situation for *Pleuromeia* is not entirely clear from the evidence Retallack presented. For organic remains, as with inorganic clastic particles, a resulting assemblage may merely reflect the characteristics of the sediment supply. If *Pleuromeia* stands formed the dominant vegetation over large areas within the drainage basin, they would also, inevitably, form the dominant fossils in a range of depositional settings. Such an example is often provided by *Equisetum* in Mesozoic rocks. Accordingly, the reconstruction in Figure 1 presents *Pleuromeia* as a plant of freshwater clastic swamps rather than coastal brackish ones. Whether such places in the Triassic may have been saline in the sense that inland lakes of arid regions today can be saline is not addressed. It is clear that *Pleuromeia* grew in inorganic clastic, rather than organic-rich, dominated swamps.

CYLOSTROBUS-SKILLIOSTROBUS-TOMIODENDRON-LYCOSTROBUS

A number of large cones and stem remains, known best from the Southern Hemisphere, have been described. Currently, the most useful account is that of Ash (1979) for *Skilliostrobus*. Known essentially from isolated rounded to ovate strobili, *Skilliostrobus* contrasts markedly in shape and sporophyll form with the more elongate strobili of *Pleuromeia*. They were heterosporous and bisporangiate, and the wedge-shaped unisporangiate sporophylls bore, in *Skilliostrobus* and in some of the species referred to *Tomiostrobus*, a narrow distal limb unlike sporophylls of *Pleuromeia*. Some of the figured sporophylls look remarkably like *Isoetes* sporophyll bases (Neuburg, 1936).

The in situ megaspores of *Skilliostrobus* appear similar to *Horstisporites/Maiturisporites* and the monolete microspores are of *Aratrisporites* type as in *Annalepis*, both types of spores being quite unlike those of *Pleuromeia*. Whether *Skilliostrobus* strobili were genuinely pedunculate as de-
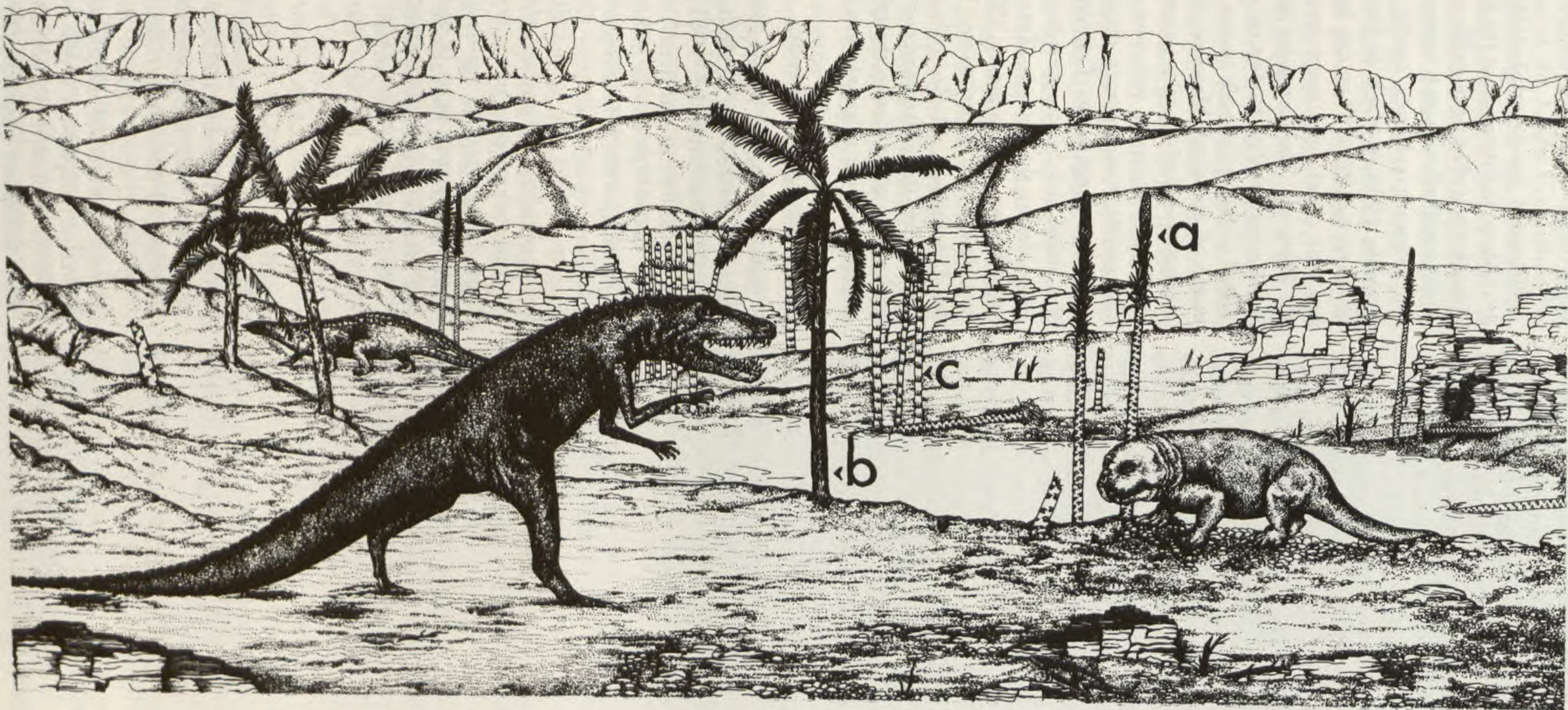
FIGURE 1. Reconstruction of Triassic landscape showing *Pleuromeia* (a) in its likely habitat, together with *Leptocycas* (b) and *Equisetum* (c). Drawing by P. Laird based on information collated by C. R. Hill.

scribed by Ash is, we believe, unlikely. As is often the state of preservation in *Pleuromeia*, *Skilliostrobus* may have been borne on a broader axis than figured by Ash, with a wide cortex that tended to rot away, leaving the woody stele in the center. Mature strobili may have been abscised, as appears to have been the case in *Pleuromeia*.

It is likely that the structure described by Chaloner & Turner (1987) from Queensland is a denuded permineralized cone of *Skilliostrobus* type. Comparable structurally preserved material currently under study by D. Cantrill, Melbourne, will undoubtedly advance our knowledge of Australian Triassic lycopsids. This material may help to clarify the uncertain relationship of *Skilliostrobus* to the other large, similar but more elongate Triassic cones and plants from the Southern Hemisphere. One of these plants is described under the name "*Pleuromeia longicaulis* (Burges)" by Retallack (1975), which has stems of broadly pleuromeian/*Nathorstiana* type, up to ca. 1 m long and ca. 2.5 (?) cm broad. Others are *Cylostrobus* Helby & Martin and *Cylomeia* White. White (1981) illustrated a series of fine vegetative specimens bearing long microphylls that in one species appear to have been clearly trabeculate as in *Isoetes*. She presented evidence that the leafy stems bore *Cylostrobus* strobili, with which they are intimately associated, at their apices. It should be noted that this material is well preserved, with in situ spores (Helby & Martin, 1965). It clearly deserves further detailed study using modern techniques and thorough nomenclatural revision.

In comparison to this promising Australian material, most other records of similar-looking strobilar fragments and isolated sporophylls are of relatively little significance as presently described (see e.g., Sadovnikov, 1982, and Neuburg, 1936) except as indicators of geographical distribution. Sadovnikov (1982) assigned *Skilliostrobus* to *Tomiostrobus* without any evidence other than broad similarity in morphology of the sporophylls. Nevertheless, some of the Russian specimens do indicate the widespread occurrence of material broadly like that from Australia. *Austrostrobus ornatum* is a strobilus from Argentina described by Morbelli & Petriella (1973), which is undoubtedly similar to *Cylostrobus* and the two genera were formally synonymized by Retallack (1975).

Nathorst's (1908) beautifully illustrated *Lycostrobus scottii* from the Rhaetic (or Liassic) of Sweden (see Chaloner & Boureau, 1967) is a cylindrical strobilus with highly distinctive megaspores unlike those of the Australian material. It also deserves additional study.

SPORE DATA: DISPERSED SPORES

Dispersed spores attributable to the lycopsids are widespread throughout the Mesozoic. Although quantitatively they are usually a minor component of the total palynomorph assemblage, they are often biostratigraphically useful (Traverse, 1988; Kovach, 1988; Kovach & Batten, 1989; Batten & Kovach, 1990). They can be locally abundant, but they never form spore-dominated coals as in the Paleozoic. The increasing quality of the megafossil record and of studies on in situ spores contained within megafossils means that an increasing range of dispersed Mesozoic spores can now be attributed directly to the parent plants. Thus, of the Triassic lycopsids reviewed above, several species enable contemporary dispersed spores to be related to megafossils. Conversely, for example, the global and biostratigraphically limited occurrence during the Triassic (Traverse, 1988; Grauvogel-Stamm & Duringer, 1983) of the cavate monolete spore *Aratritriletes* Leschik (produced by *Cylostrobus*, *Skilliostrobus*, and *Annalepis*) underscores the widespread occurrence of the various parent plants, even though their megafossils are known from relatively few localities.

MEGASPORES AND MICROSPORES

Several dispersed megaspore genera that have been used extensively in Mesozoic biostratigraphy (see e.g., Marcinkiewicz, 1981; Fuglewicz, 1980) are now known in situ from Triassic material, notably: *Tennellisporites* (in *Annalepis* from France); *Dijkstraisporites*, *Banksisporites*, and *Laevigatisporites* (*Annalepis* from China, see Wang & Lou, 1990); *Horstisporites* and *Maiturisporites* (in *Skilliostrobus*); and *Banksisporites* (from *Cylostrobus*). In addition, Scott & Playford (1985) reported occurrences of *Aratrisporites* microspores attached to the surfaces of *Banksisporites* and *Nathorstisporites* dispersed megaspores.

The position in the Jurassic and Cretaceous is less satisfactory because relatively few lycopsid spores of the later Mesozoic have been linked directly to megafossils as in situ occurrences, principally the megaspore *Minerisporites* to *Isoetites* megafossils, and various trilete small spores named *Lycospora* (Traverse, 1988) or *Lycopodiumsporites* (Couper, 1953). Monolete dispersed spores have been named *Monolites* (Couper, 1953).

However, since most of the currently known Jurassic–Cretaceous megafossils are fairly similar to extant lycopsids, it is also reasonable to take a different approach: to postulate affinities of the dispersed spores *indirectly*, by reference to in situ

spores of the extant taxa, such as Hueber (1982) did for megaspores of the Lower Cretaceous Potomac Group. Such comparison has been undertaken with increasing precision in recent years by Batten (1988), Kovach & Dilcher (1988), Kovach (1989), and Koppelhus & Batten (1989). As Batten has pointed out, the problems in this regard are illuminating in that they reflect as much on the current limited state of knowledge of extant spores as on that of the fossils. Moreover, particular problems arise with extant *Isoetes*, in which the megaspores may possess a silicified perispore that is often not preserved in fossil megaspores. Thus, although there are several exemplary studies of the megaspores of the extant plants (e.g., by Hickey, 1986a), the data are rarely in a form suitable for comparison with fossil spores and vice versa (see also Pant & Srivastava, 1962). Added to this, in past treatments of the extant spores (and to an extent of fossil ones following the system of Potonié, 1956), a narrow range of such characters as surface sculpture has been emphasized at the expense of other characters with the predictably unfortunate consequence of holding up scientific progress for many years (Hickey, 1986a). Once a wider range of characters was employed an important biological reality became clear, that megaspore variation in *Isoetes* can be considerable within "species" and within populations, leading to convergence of spore characters in many cases. The biological basis for this lies in growing chromosomal, ecological, and morphological evidence for frequent hybridization and allopolyploid speciation indicating a highly complex evolutionary history for *Isoetes*. This is only now beginning to be clarified (Hickey, 1986b; Hickey et al., 1989; Taylor & Hickey, 1992). Additional work is needed on extant spores in the context of this growing knowledge of the biological relationships of *Isoetes*, with reference to a wide range of spore characters such as the "secondary ornamentation" features referred to by Hickey (1986a) as well as to those of surface sculpture, and, if comparisons with fossil spores are to be effective, both before and after removal of the siliceous perispore with hydrofluoric acid.

A more sophisticated recent approach by leading fossil megaspore workers is a critical assessment of the infrastructure of lycopsid megaspore exines. Stimulated by pioneering transmission electron microscope (TEM) studies of sectioned extant material, undertaken in Europe during the 1960s and 1970s by Martens, Pettitt, and Stainier (see Koppelhus & Batten, 1989, for references), Kovach and Batten have recognized that a fundamental difference in exospore construction exists between megaspores of extant *Isoetes* and selaginellaleans at the ultrastructural level. In *Isoetes* the megaspore exospore is composed dominantly of a three-dimensional reticulate network of threads in which the main orientation of the threads and airpores between them is more or less parallel with the spore surface, whereas in selaginellaleans much of the exposure is usually constructed from a mesh of tightly packed threads and/or robust rods, with less intervening porespace than in *Isoetes* exospores and with the elements at more variable angles to the spore surface. Additionally, in some selaginellaleans the exospore is constructed of tightly packed granules that are organized into distinctive geometrical patterns (Kovach & Batten, 1989).

Kovach (1989) described a relatively simple laboratory procedure for obtaining megaspore exospore sections for examination by scanning electron microscopy (SEM). Using such sections he selected two consistently measurable infrastructural characters for quantitative study: (a) porosity, and (b) variability in orientation of the elongate pores (airspaces)—measured as angles relative to a baseline drawn perpendicular to the spore surface. The results indicate consistently higher dispersion of angle of the pores around the mean (= lower r values) and consistently lower porosities in a sample of extant selaginellalean versus *Isoetes* megaspores. Differences in the r values appear to be more powerfully diagnostic than porosity. Kovach showed that two Cretaceous dispersed megaspore genera relate as would be expected on the basis of general morphological comparisons with extant species: *Erlansonisporites* to the extant selaginellaleans and *Paxillitriletes* to extant *Isoetes* (Kovach & Dilcher, 1985; Kovach, 1989).

Utilizing such approaches, together with other indirect indicators (for example, occurrence of associated or adherent microspores—monolete in *Isoetes*, trilete in selaginellaleans), Jurassic and Cretaceous megaspores can now be attributed as shown in Table 1.

As Batten (1988) pointed out, some megaspores regarded as probably selaginellalean are zonate, that is, they have an equatorial flange as in *Isoetes* and therefore their general morphology resembles that of *Minerisporites* and *Henrisporites*. This underscores that the kind of convergence in characters detected among species within extant genera may also apply between genera in the fossil record. In this respect the ultrastructural evidence appears to take on added significance.

Table 1 is not intended to be exhaustive, and it refers mainly to Cretaceous taxa. However, it presents a start that we hope will be built on rapidly

TABLE 1. Megaspores attributable to lycopsid orders.

Isoetaleans, sens. lat.	Selaginellaleans
Minerisporites (including M. mirabilis and Mineri-sporites species A known in situ)	Erlansonisporites (E. spinosus, E. erlansonii, E. scanicus, E. septus, E. sparassis; see Harris, 1961)
Dijkstraisporites	Ricinospora cryptoreticulata
Henrisporites	Thylakosporites retiarius
Herbosisporites	Rugotriletes diktyotus
Paxillitriletes (including P. phyllicus; see Harris, 1961: 44)	Rugotriletes costatus
Sepisporites	Trileites persimilis, known in situ
Tenellisporites pro parte	Trileites murrayi (Harris, 1961: 44)
Scabratriletes pro parte	Cabochonicus carbunculus
	Verrutriletes dubius
	Verrutriletes compostipunctatus
	Bacutriletes nanus
	Bacutriletes majorinus
	Horstisporites species
	"Triletes" onodios (Harris, 1961)

in the future. Although inadequate, it summarizes the considerable recent progress that has been made, representing a broad attribution of some 17 out of the 70 or so Mesozoic genera of dispersed megaspores that have been recognized to date. Since several of these 70 genera represent plants other than lycopsids (mainly water ferns), the 17 genera probably represent about a third of the known lycopsid megaspore diversity. It is interesting to compare this general picture emerging today with that of Harris (1961), who was unable to attribute any of the Yorkshire Jurassic megaspores other than in the broadest of terms.

Environmental significance. Harris (1961) pointed out that dispersed megaspores are moderately abundant in Yorkshire Jurassic plant localities. Although few megafossils are known from Yorkshire, the nonuniform megaspore composition of the localities suggests that the parent plants did not live far from the various coastal plain environments in which they were deposited. Batten (Koppelhus & Batten, 1989) noted that in horizons with podsols and evidence of fluvial activity, inferred selaginellalean megaspores are the most abundant spores, indicating a likely growth environment that could have ranged from low-growing streamside vegetation to nearby interfluvial forest or scrub environments, directly comparable to environments occupied by most selaginellalean species today. Probable *Isoetes*-group megaspores were associated with low energy environments of deposition; the inferred parent plants and the sedimentological evidence both indicate that the plants lived in a floodplain marsh to lacustrine habitat as occupied by *Isoetes* today. Significantly, Batten drew attention to the fact that several megaspore

genera attributed to *Isoetes*-like plants can occur locally in large numbers in Cretaceous sediments known to have accumulated in freshwater, suggesting a likely freshwater environment of growth for the parent plants. This view is supported by occurrences of little-drifted megafossil remains as virtually whole plants in such environments, e.g., *Isoetites choffatii* (see below) and *Isoetites* sp. nov. (see below), that are very similar to species growing today in freshwater.

MIOSPORES

Miospores attributable to the lycopsids are found in almost all the Mesozoic strata that have been analyzed for spores and pollen. Although usually a minor component of the flora, they are present throughout the world and apparently occur in most of the examined deposits. For example, some reports of the Cretaceous miospores from various areas are eastern Australia (Cookson & Dettman, 1958), southeastern Australia (Dettman, 1963), western Canada (Singh, 1964, 1971), southeastern United States (Phillips & Felix, 1971), and New Zealand (Couper, 1953). Because the host plants rely mainly on wind dispersal, the worldwide distribution of their miospores (spores in the case of Lycopodiales and microspores in the case of Selaginellales) is not surprising. For most of these miospores the host plants are unknown and, in view of the depauperate record of fertile lycopsid remains in the Mesozoic, there is probably little hope of assignment to host plants for these spores until modern approaches similar to those utilized for megaspores are attempted. The main Sporae Dispersae genera that have been recognized as spores

of lycopsids are *Lycopodiumsporites, Lycospora, Lycopodiacidites, Reticulatisporites* (Phillips & Felix, 1971), and *Acanthotriletes* for *Selaginella* (Singh, 1964). These genera appear in most of the spore references where lycopsid spores have been described.

Spore data thus show that the three lycopsid lines continue throughout the Mesozoic worldwide as a minor component of the flora, but as yet give no clues regarding significant evolutionary changes in the groups.

HERBACEOUS FORMS

Many herbaceous forms similar to those of extant lycopodialeans and selaginellaleans have been described from the Carboniferous onward (Thomas, 1992). However, the Mesozoic fossils either rarely preserve sufficient detailed information of the kind required for accurate identification, or have not been studied sufficiently to illustrate such details. There is real danger of confusion of isophyllous forms with conifer shoots, fern rhizomes, and bryophytes (Seward, 1910: 74–75), and also a frequent inability to tell whether the material was lycopodialean as distinct from selaginellalean. As is the situation for Mesozoic lycopsid megaspores discussed above, the generally limited state of present knowledge of these forms necessitates heavy reliance on characters of the extant taxa—for example, that selaginellaleans have ligulate leaves and sporophylls whereas lycopodialeans lack ligules, and that selaginellaleans are heterosporous with usually four megaspores per megasporangium whereas lycopodialeans are isosporous. In all extant species of these orders the isospores or microspores are trilete, as opposed to the monolete microspores of *Isoetes*-like forms. There are also a number of detailed vegetative differences, although both of the living orders include some forms that are isophyllous, considered the plesiomorphic condition for lycopodialeans by Øllgaard (1987), as well as a range of more or less anisophyllous ones, although selaginellaleans are usually more regularly anisophyllous (Harris, 1961).

Heavy reliance on comparison with extant forms inevitably means that the law of the excluded middle applies (Davis & Heywood, 1963: 34–35; Hill & Crane, 1982: 322–324), such that any genuinely intermediate forms might well be overlooked by being forced into a category, i.e., selaginellalean versus lycopodialean, in which they do not really belong. Additionally, where detailed preservation of vegetative characters is limited, which is often the case, there is a marked asymmetry in ability

to recognize Selaginellales when relying on spore characters. Thus, the occurrence of in situ megaspores is a clear indication of selaginellalean affinity, whereas if only small spores (miospores) with trilete laesurae are found (especially if they are poorly preserved) they could indicate identity of the parent plant as either lycopodialean or selaginellalean.

LYCOPODIALEAN LINE

Because of the fragmentary condition of these plants when found as fossils, few of the characters considered important by Øllgaard (1987, 1989) in classifying extant lycopodialeans can be recognized in fossil material. These characters relate to branching pattern (isotomous, anisotomous, flabellate), stem and rhizome anatomy, sporophylls (paleate to peltate) with a sporangium near the axil that may be displaced, and sporangia of equal valves or unequal valves, in addition to particular characters of leaf variability such as those to do with leaf form and attachment mentioned above. Adding these to the considerations already mentioned, it is hardly surprising that there are currently no unequivocal records of Mesozoic lycopodialeans, and none that can be characterized in terms of the genera now in use for extant lycopodialeans. If anything, it is perhaps surprising that at least a few are convincingly, even if not certainly, lycopodialean in a broad sense.

The quality of these records ranges widely. At worst are those such as "*Lycopodium* sp." of Drinnan & Chambers (1986) from the early Cretaceous of Victoria, which appears to have no characters diagnostic of Lycopodiales. A number of other species known solely as vegetative material are lycopsids and may be lycopodialean, but detailed evidence is lacking: anisophyllous species such as *Lycopodites victoriae* of Seward (1904) from the Jurassic of Victoria, and isophyllous ones such as *L. arberi* Edwards from the Jurassic of New Zealand (Edwards, 1934), and *L. sewardi* Nathorst from the Mesozoic of Spitzbergen (Nathorst, 1897). Some other occurrences of anisophyllous forms, such as *Lycopodites gracilis* from the Mesozoic of India figured by Seward & Sahni (1920), are similar to *L. falcatus* from the Yorkshire Jurassic, discussed below, and thus can also probably be considered lycopodialean. Moreover, *L. gracilis* occurs in the same series of beds as small, 2-mm-wide axes named *Lycoxylon*, which have distinctly lycopodialean anatomy (Srivastava, 1946).

To our knowledge, this leaves few species of

FIGURE 2. *Lycopodites falcatus* Lindley & Hutton. Holotype of Lindley & Hutton (1831–1833) volume I, plate LXI, figures 1,2. Specimen v. 39314 in British Museum (Natural History).

compression fossils that can be accepted on currently available evidence as definitely lycopodialean. The best known is *Lycopodites falcatus* Lindley & Hutton (Fig. 2), which was described and discussed in depth by Harris (1961). It has isophyllous main stems up to 2 mm wide, bearing dichotomizing branches that are complanate and distinctly anisophyllous. Like extant genera of lycopodialeans but unlike extant selaginellaleans, there is no leaf in the angles of dichotomy of the branches; there is a lower number of small versus the larger leaves; the shape and attachment of the large lateral leaves is as in lycopodialeans, to reiterate Harris's words, "entirely foreign to *Selaginella*," as is the broad distribution of the leaf stomata (see also Thomas & Masarati, 1982). However, the exact combination of vegetative characters seen in *L. falcatus* is not one that is seen among extant lycopodialeans. It is also significant that strobilar material is poorly known even for this otherwise

well-characterized species. Harris described some detached strobili in close association with the vegetative branches, but while they are broadly lycopodialean in appearance they are poorly preserved and have yielded only a few spores on maceration. A comparable strobilus in attachment to vegetative shoots has been illustrated by Hill et al. (1985). This may prove to yield spores, although morphologically it too is poorly preserved. Further collecting is required if knowledge of this "classic" but incompletely known species is to be improved. This species has been proposed as the basis for conservation of the generic name (Pal & Ghosh, 1990).

Another convincing record of a complanate but isophyllous lycopodialean is *Lycopodites multifurcatus* of Li et al. (1986, excluding their pl. 38, figs. 3, 3a), from the early Cretaceous of northeastern China. As in the Yorkshire Jurassic species, preservation is sufficiently good to be certain that

leaves are lacking from the angles of dichotomy of the branches. The main stems and strobili are not known.

Skog (1986, 1990) has described *Wathenia*, another complanate isophyllous form. It is based on some newly collected material from the English early Cretaceous and on some formerly attributed to *Hymenopteris psilotoides*. Other specimens referred to *Onychiopsis psilotoides*, but probably representing the German and Japanese material of *O. elongata* Yokoyama, have been recognized as a dicksoniaceous fern by Friis & Pedersen (1990). If *Wathenia* is actually a lycopodialean, then it is of considerable interest in representing a possibly epiphytic species resembling extant species from the tropics. Certainly the combination of characters is of an advanced complex close to modern species of *Lycopodium* and *Huperzia*, and not of the generalized type associated with those extant species considered primitive by workers such as Øll-gaard. The fertile phyllotaxis of the somewhat flattened branches is helical, sporophylls are paleate, and the spores, numbering about 200 per sporangium, are similar in structure to those of extant lycopodialeans. Sporangia are elongate, a condition not known in extant lycopodialeans but found in selaginellaleans. As with *Lycopodites falcatus*, there is a hint from this fossil of characters that are intermediate between those of extant selaginellaleans and lycopodialeans.

Finally, Harris's (1976) *Lycopodites hannahensis*, if correctly attributed, would greatly extend the scope of lycopodialeans to encompass slender, upright, evidently aquatic plants—unlike any surviving today. While Thomas (1992) accepts *L. hannahensis* as convincingly lycopodlike and believes that comparable forms occur in the Jurassic, we are inclined to be more skeptical. The material is exceedingly poorly preserved and compares favorably in almost every respect with vertical in situ roots known to have been produced by fossil *Equisetum* species, especially *E. columnare* (Harris, 1961). In the field such roots often appear to branch upward as in *L. hannahensis*, but when traced a sufficient distance in the rock they converge again at a higher level; we suggest that this represents the effects of decay of the roots into separate strings that then were pulled apart by soft sediment. Whatever the merits of our suggestion or of Thomas's appraisal, however, insufficient knowledge exists to make a firm judgment at this time; further study material based on additional carefully controlled collecting, together with detailed evaluation of extant *Equisetum* rooting systems, is required.

The meager fossil record of Mesozoic lycopodialeans indicates that new forms were appearing at the end of the Jurassic and through the Cretaceous. We hypothesize that the modern lines of lycopodialeans were established during late Jurassic–Cretaceous times and that their diversity today may result from the same events which led to the increasing diversity of the angiosperms and the modern fern families (i.e., Polypodiaceae). Many of the modern lycopodialeans are associated with angiosperm dominants as terrestrial or epiphytic plants. While the fossil record is not strongly supportive of such a hypothesis, it does not negate it. Much more work with existing and new collections is needed on the critical ages of the late Jurassic and Cretaceous with the lycopodialeans in mind.

SELAGINELLALEAN LINE

Evidence for herbaceous, ligulate, and heterosporous forms, often attributed to the genus *Selaginellites*, occurs from the Carboniferous onward. The general situation of Mesozoic selaginellaleans is similar to that of lycopodialeans in that a number of forms comparable with living ones are known, but few are exactly like any living species or group of species. A few, such as *Synlycostrobus* and *Lycopodites macrostomus*, are unlike any extant members. The situation is a little more satisfactory than for lycopodialeans partly because it is based on more definitive evidence of ligules, strobili, and spores.

Isophyllous forms similar to *Huperzia selaginoides*, such as *Selaginella harrisiana* from the Permian of Australia (described in detail by Townrow, 1968), were clearly well established by the outset of the Mesozoic. Townrow's material is important because it has a long, apparently leafless rhizome like that of *Asteroxylon*, corroborating Karrfalt's (1981) view based on developmental anatomy that the rooting pattern of extant species of *Huperzia selaginoides* type is highly derived rather than representing the generalized condition. Subsequently, critically recognizable isophyllous forms are unknown until the occurrence of *Lycopodites macrostomus* Krassilov from the middle Jurassic (Callovian) of Siberia (Krassilov, 1978). This species is well preserved, with evidently ligulate leaves, although details of the ligulelike structures are obscure. Epidermal features, however, are clearly illustrated by Krassilov. This species is interesting in that the shoot morphology, the lack of a leaf in the angle of shoot dichotomy, and the distribution of stomata scattered over both surfaces of the leaf are distinctly lycopodialean rather than

selaginellalean in terms of extant analogues. Unfortunately, the strobilus and spores are as yet unknown or unrecognized. We include *L. macrostomus* here under Selaginellales purely because by reference to extant species the law of the excluded middle could be taken to enforce consideration of all such ligulate Mesozoic lycopsids as selaginellalean. However, such a view is not favored by the balance of the evidence, as Krassilov pointed out; we might just as appropriately have included this species under Lycopodiales. Moreover, studies of the Devonian *Leclerqia* have made clear that there are other ancient plants with strongly lycopodialean characteristics that possessed a ligule (Grierson & Bonamo, 1979).

Judging by the currently available evidence, *Lycopodites macrostomus* is of considerable importance in demonstrating that at least in their vegetative characteristics the selaginellalean and lycopodialean clades were not yet fully distinct in the Jurassic. In other words, this species appears to represent an important missing link between the two clades. It underscores the importance of finding well-preserved strobilar material of both *L. macrostomus* and *L. falcatus* if we are to obtain a better overview of lycopodialean/selaginellalean relationships.

Vegetative material considered to represent an isophyllous lycopsid from the middle Jurassic (Aalenian), which Black (1934a, b) collected from Loftus Alum Quarry in Yorkshire and described under the name of the coniferous shoots *Pagiophyllum peregrinum*, was mentioned by Harris (1979: 57). Although morphologically broadly resembling *P. peregrinum*, Harris recognized that Black's material is very different from that species, not least in failing to yield a cuticle on maceration, and he indicated possible lycopsid affinity. A well-preserved portion of shoot from additional material, collected by C. Hill and Ronald Williams at Loftus Alum Quarry in 1984, is illustrated here in Figure 3, showing coaly spots suggestive of ligule pits situated near the bases of the leaflike appendages. Further study of this material, however, has shown that the appendages in Figure 3, which look broadly like *Pagiophyllum* or lycopsid leaves, are, in fact, the scaly bases of quite different organs. As illustrated, they closely resemble scaly appendages on osmundaceous fern stems and rhizomes attributed to *Todites princeps* (Schweitzer, 1978). The appendages narrow at their apices and are produced into elongate petiolar extensions several centimeters long. The surface throughout the scaly bases and these apical extensions shows only uniformly narrow elongate cells and lacks any evidence of

midrib or stomata. Two other factors that also argue against a lycopsid affinity are the steeply inclined spiral of attachment of the scales (low spirals are typical of lycopsids), and the position of the apparent ligule pits, which is too low in relation to the free part of the appendages to fit any known lycopsid. These probably represent points where roots left the rhizome. When compressed vertically they would form coaly plugs.

All other Mesozoic records of selaginellaleans known to us represent anisophyllous or vegetatively indeterminate forms. One of the best preserved and best described is *Selaginella anasazia* Ash from the late Triassic of Arizona (Ash, 1972). The dichotomizing branches bore leaves like those of many living species in four ranks, two ranks of large spreading leaves up to 2.3 mm long and two of small leaves up to 1.2 mm long. The leaves are so well preserved that tracheid anatomy of the midvein and epidermal details of the lamina could be illustrated clearly. The leaf form resembles that of extant species such as *S. krausiana* and *S. abysinica*, which today live in moderately moist shady habitats. Although the strobili of *S. anasazia* are poorly preserved, they include in situ megaspores and, like the vegetative shoots, appear to resemble those of extant Selaginellales.

Other well-preserved late Triassic material from Sweden, named *Selaginella hallei*, was studied by Lundblad (1950b) based on anisophyllous shoots bearing leaves in four ranks. Attached strobili bore sporophylls in a tightly imbricate spiral as occurs in some extant species. They were heterosporous, with four megaspores per megasporangium as in most extant species; microspores were trilete with an annular ring, which is also characteristic of such extant species as *S. scandens* and *S. parkeri*. The megaspores are attributable to *Trileites persimilis*.

Lundblad (1950a) also described other broadly comparable vegetative material as *Lycopodites scanicus*, which requires revision using modern techniques. There is some indication from her illustrations that vegetative branches attributable or potentially attributable to *S. hallei* may have been variable in form, ranging from 4-ranked anisophyllous to isophyllous with the leaves in an imbricate spiral; if not, it would appear that distinct isophyllous selaginellaleans may have occurred in the same deposits. In either case, additional knowledge would be of considerable value in clarifying relationships between the Swedish material and extant species.

We include mention here of an isolated strobilus yielding spores, named *Selaginellites polaris* by Lundblad (1948). This is more for completeness

of coverage than from the conviction that on present evidence it is better placed here than with the subarborescent lycopsids we reviewed earlier in this paper (see also Chaloner & Boureau, 1967, for discussion).

Fossils closely resembling anisophyllous selaginellaleans do not reappear significantly in the fossil record until the early Cretaceous, when there is evidence of considerable diversity. Watson's (1969) revision of *Selaginellites dawsoni* from the English Wealden demonstrated heterospory and showed that the megasporangia had four megaspores. Material was not abundant, and no spore relationships were suggested. Comparisons were made with extant *Selaginella sanguinolenta* and *S. emmeliana*, although the fossil is not identical with either species in all its characters. Most other Cretaceous species of *Selaginellites* are vegetative shoots with a leaf arrangement that suggests assignment to *Selaginella* rather than *Lycopodium* (see also Seward, 1910, 1913). Many are poorly preserved fragments. One such example, *Selaginellites marylandica* Fontaine (Ward, 1905), was apparently so poorly preserved that it can no longer be found in the collections at the United States National Museum of Natural History.

As part of the work for this review, J. Skog has reexamined a strobilus of early Cretaceous age from South Carolina described by Berry (1910) as *Lycopodium cretaceum*. Although Berry described 17 specimens in his paper, only the one illustrated here in Figure 4 remains in the collections today. His description of the sporophylls appears to be more or less accurate, but the specimen has suffered degradation over time and now the specimen is too poorly preserved to confirm the accuracy of his description. The sporangia are attached to the leaves in Berry's reconstruction, but he indicates that the drawings are "somewhat diagrammatical." In our opinion, it is impossible to confirm the position of the sporangia on the sporophylls or whether they are borne on stalks (Figs. 5, 6). Sporophylls are thicker at the base and acute at the apex (Fig. 5). Careful examination of the strobilus reveals that there are poorly preserved large dark areas among the leaves (Fig. 6), and these rounded areas may be the sporangia that Berry reconstructed. Material that appears to be carbonized from these areas has been removed and prepared in different ways. Attempts to extract spores were unsuccessful. Part of the material was placed in hydrofluoric acid to see if any plant material could be isolated, but only small fragments appeared. These have been removed and examined with light and scanning electron microscopy (Figs. 7–9). Because of the poor
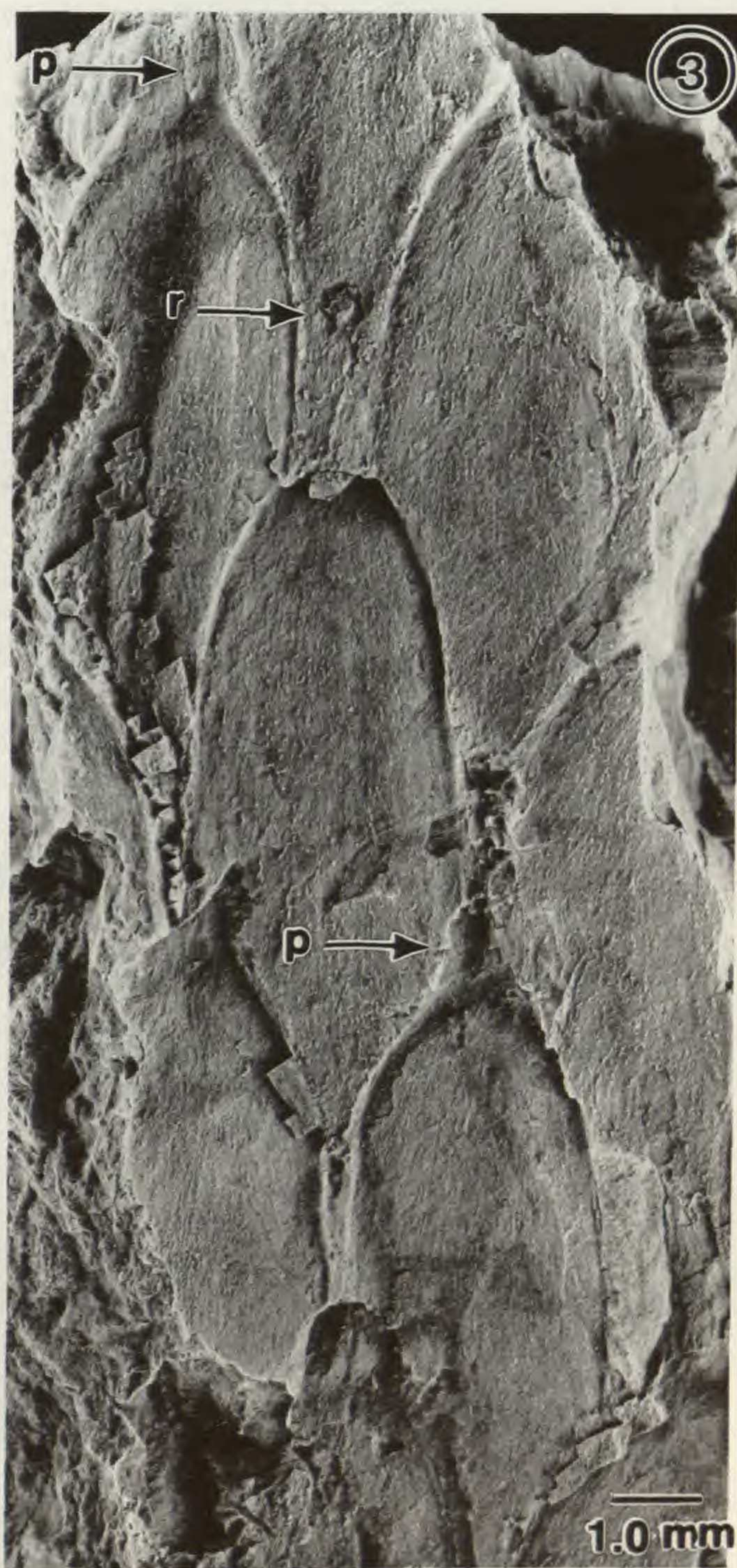

FIGURE 3. Lycopodlike axis from Loftus Alum quarry, interpreted here as a fern stem. British Museum specimen v. 63453. (p) = petiolar extensions; (r) = coaly plug probably the site of a root.

preservation, assignment is questionable at best. The structure they most resemble, although they are clearly different and smaller, is the palynomorph *Dictyothylakos* Horst (1954), described from the Cretaceous by a number of authors (Hughes, 1955; Singh, 1964; Kovach & Dilcher, 1988; Hueber, 1982). Hueber's description includes SEM illustrations, which are comparable to the SEM material here. The network of primary strands reinforced by secondary strands characteristic of Hueber's material can be seen in Figure 9 (arrow). The material here is much smaller than
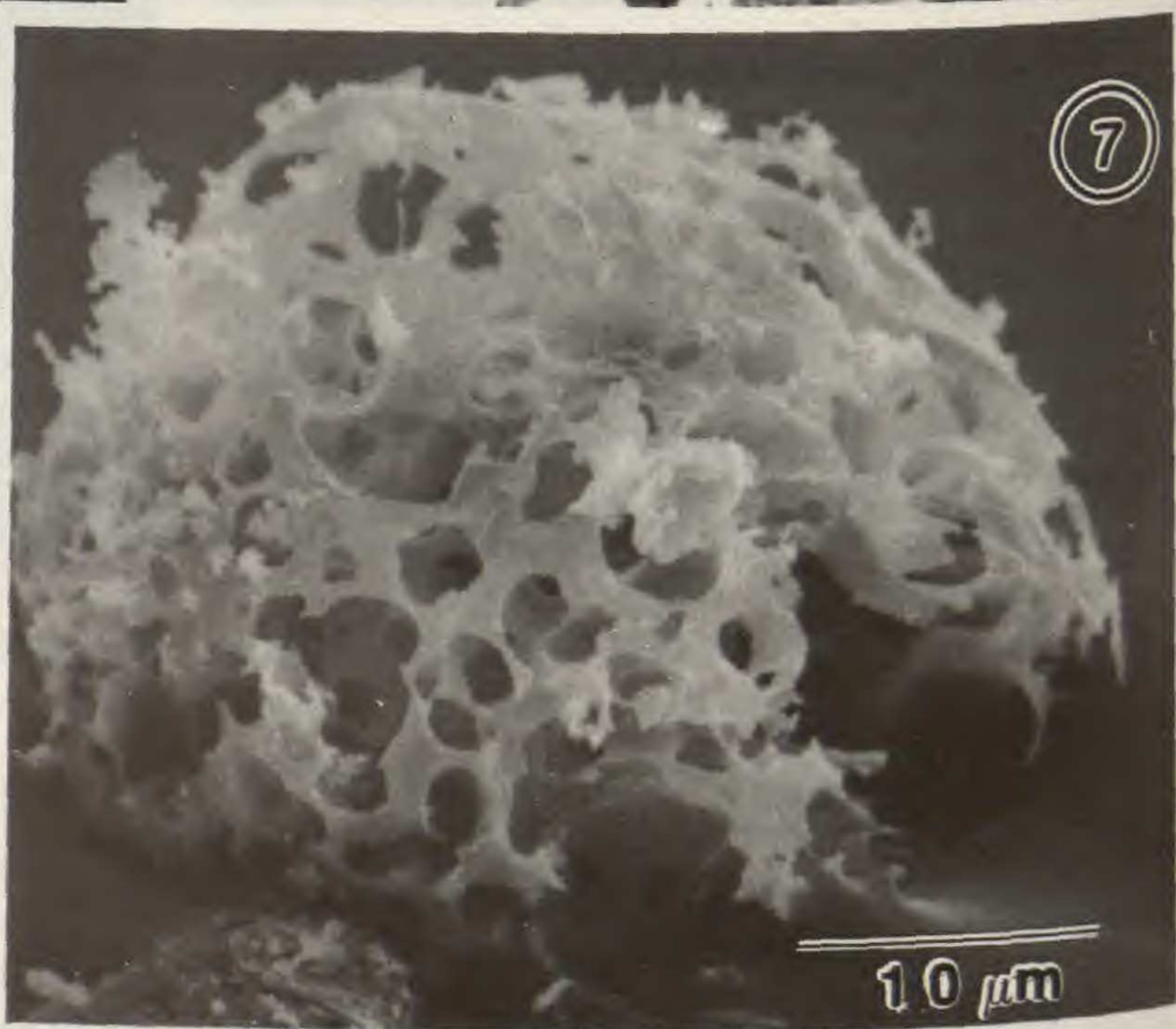
that of Hueber, but since these represent fragments the size is not critical. However, Hueber's material is flat and not rounded, and the material extracted from *Lycopodium cretaceum* appears to be a round structure (Figs. 7, 8). Hueber suggested it could represent the operculum of a selaginellalean sporangium, since the similarity in ornamentation and structure to parts of the spore *Thylakosporites* were obvious not only to him but to Hughes (1955). The granular surface is evident in the material shown in Figure 9. Because the material seen here was obtained from a lycopodiaceous strobilus and isolated from the region of the putative sporangia, the suggested identity with the lycopsids may be more substantiated, but the structure remains as elusive as ever. It probably represents some part of a degraded lycopsid strobilus, but whether operculum, spore, or cuticular portion of the wall is not clear. This material illustrates that even when modern techniques are utilized some poorly preserved material remains enigmatic.

As presently described, *Limnothetis gobiensis* of Krassilov (1982) from the early Cretaceous of Mongolia is another enigmatic, poorly preserved lycopsid. Krassilov reconstructed the vegetative shoots as bearing ligulate leaves, isophyllous and two-ranked on main axes and anisophyllous, four-ranked on lateral branches (with two sets of broadly ovate imbricate leaves and two of small pointed leaves). He reconstructed the fertile zones of these branches (there appear to be no definite strobili) as bearing crowded lateral condensed branches, each in turn bearing a single terminal sporangium surrounded by pointed leaves. The sporangia are stated to be dimorphous. Presumed megaspores (occurring in association and not in situ) are large and have a regularly reticulate sculpture; microspores are stated to be trilete and apparently were extracted in situ.

It is difficult to assess this intriguing but inadequately described material. If indeed a selaginellalean it is of a highly specialized form that, like *Synlycostrobus* (see below), may be unique to Selaginellales. However Krassilov's photographic illustrations and written description do not provide evidence to justify arriving at the detailed reconstruction in his textfigure 2. On the evidence currently available the possibility cannot be excluded that the plant may be a conifer, e.g., badly preserved *Elatides* or *Geinitzia* shoots, or a pteridosperm; if it is a selaginellalean lycopsid, the fertile "short shoots" of Krassilov may actually represent germinated megaspores with small viviparous plants as occur, for example, in extant *Selaginella rupestris*.

The situation is very different for Krassilov's (1978) description of *Synlycostrobus tyrmensis* from the latest Jurassic to earliest Cretaceous of the Bureja Basin. As reconstructed from associated fertile and vegetative remains, the *Synlycostrobus* plant comprised main stems about 1 mm thick with widely spreading lateral leaves borne helically or in two ranks. The branch systems are anisophyllous and bear more closely spaced ligulate leaves in four ranks. As in extant anisophyllous selaginellaleans there are two ranks of large leaves and two of smaller ones. The fertile branches, unlike any extant selaginellalean, are compound and thus bear strobili laterally in the axils of so-called bracts or alternating with leaves, with the stalks of the strobili "fused" with the bracts. Only the microspores are known in situ; they were apparently cavate and trilete. Megaspores referable to *Bacutriletes onodios* occur monodominantly in association with the fertile shoots, including a detached megasporangium in which there are four megaspores. The strobili have paleate, keeled sporophylls, of which the detailed structure is poorly preserved, although they are typically lycopodialean/selaginellalean in form.

Although the vegetative and fertile remains of *Synlycostrobus* occur in one locality, they are preserved in different bedding planes rather than in intimate association or attachment. The possibility that the strobilar branches might have been borne on leafy shoots like those of *Lycopodites macrostomus* (although known from a different locality) cannot be ruled out; the "bracts" of *Synlycostrobus* look similar to the leaves of *L. macrostomus*. Krassilov commented, however, that occasional leaves of the strobilar branches of *Synlycostrobus* resemble those of the vegetative branches to which he attributed them.

Regardless of which vegetative shoots are the

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FIGURES 4–7. *Lycopodites cretaceum* Berry, United States National Museum specimen USNM 38199.—4. Complete specimen.—5. Enlargement of upper portion of specimen in Figure 4 showing leaves (l) in a helical arrangement, acute tips and enlarged bases of leaves and a thicker structure (t) that appears to be in the axil of the leaves.—6. Enlargement of right side of Figure 4 with leaves at the left side clearly shown. Pieces of the carbonized material in the leaf axils (arrows at center and left) were removed for microscopy.—7. Scanning electron micrograph (SEM) of round structure obtained from carbonized fragments. Three-dimensional shape can be seen in this view.
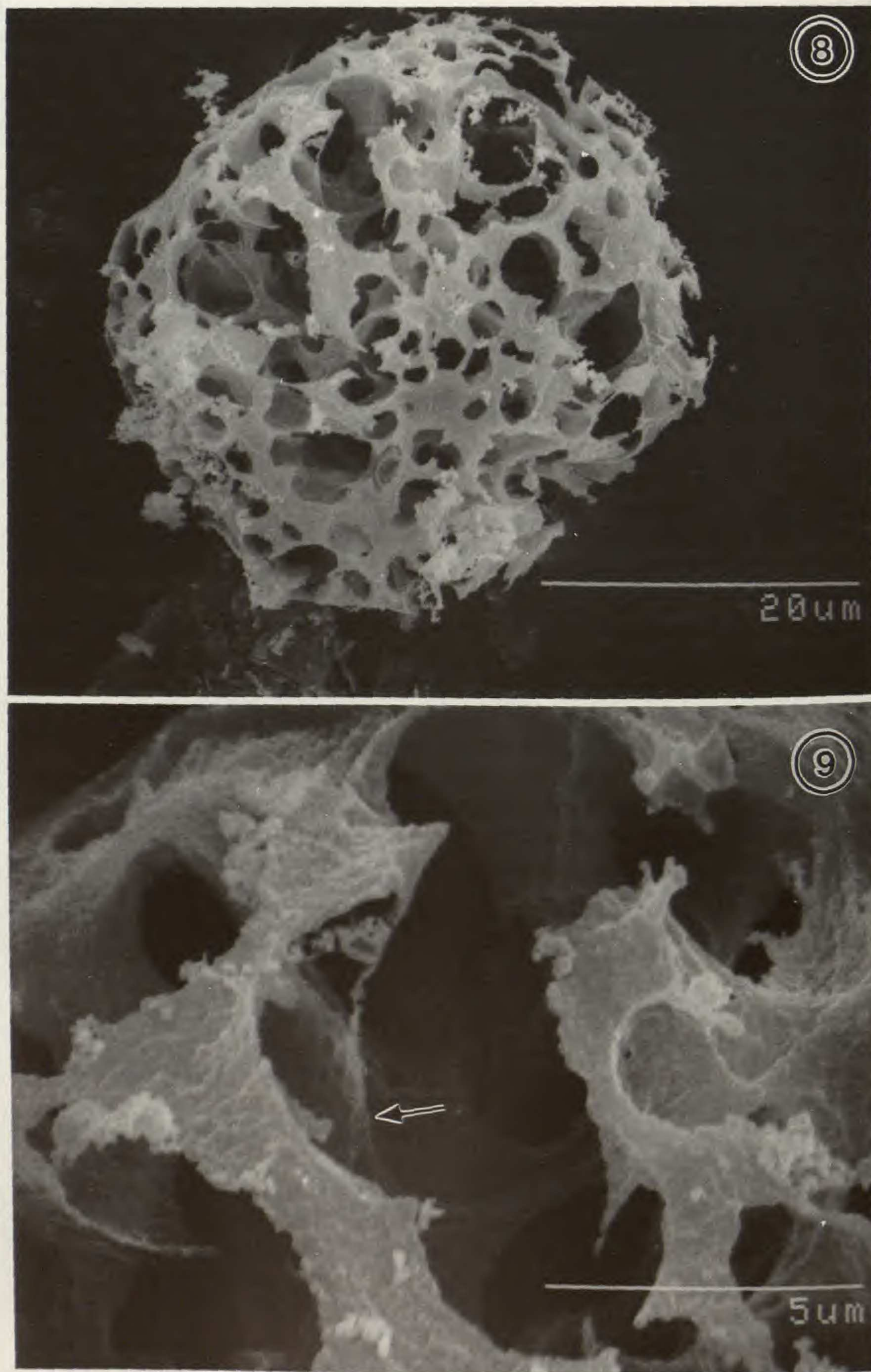
FIGURES 8, 9.   Fragmented piece of carbonized material from *Lycopodites cretaceum* Berry.—8. SEM showing network arrangement and layers of material as well as rounded shape.—9. Enlargement showing granular surface and interconnections of the network (arrow to secondary strands).

most appropriate, *Synlycostrobus* is certainly a lycopsid. As such it extends the known diversity of reproductive branch morphology within the herbaceous lycopsids, both living and fossil. Within the fertile branches, the apparent fusion of "bracts" and strobilar stalks can be interpreted as a result of condensation of a set of more elongate lateral leafy shoots, each bearing a terminal strobilus. Condensation, effectively removing nearly all the vegetative regions of the lateral axes, would bring their

terminal strobili back virtually onto the axis of the next order of branching. The length of the "bracts" is greater than that of the vegetative leaves. This length is appropriate if it represents in its proximal region a foreshortened shoot axis bearing distally a single remaining leaf; the leaf would then equate more readily in size with those on vegetative axes, and the whole "bract-like" structure thus interpreted is clearly not a bract but is itself compound, a reduced shoot. If this speculation is correct it provides an interesting parallel with the evolution of the coniferous female strobilus.

SUMMARY: LYCOPODIALEANS AND SELAGINELLALEANS

Although their fossil record offers only occasional and incomplete glimpses of these lycopsids in the Mesozoic, the fossils nonetheless represent a wide diversity of forms. There are those, especially selaginellaleans, essentially like extant species or groups of species, a situation first seen in the Paleozoic. Others, however, such as *Synlycostrobus*, and also *Limnothetis* and *Lycopodites hannahensis* if accepted as lycopsids, represent degrees of specialization unknown among extant taxa. Finally, there are those such as *Lycopodites macrostomus* that appear to provide persistent links between the two clades, even though they had begun to diverge millions of years earlier.

The environmental significance of these lycopsids is difficult to assess from the scattered records of megafossils. However, Ash (1972) pointed out that the leaf form of *Selaginella anasazia* resembles that of extant species such as *S. krausiana* and *S. abysinica*, which today live in moderately moist shady habitats. By extension and on a broadly uniformitarian basis it can be assumed that species such as *Lycopodites falcatus* probably occupied a similar habitat in the Jurassic. Most records of these forms are from mid- to high-latitude floras and few from the then-equatorial regions. Finally, an additional reason for our poor understanding or recognition of Mesozoic lycopodialeans versus selaginellaleans may be that they rarely got the chance to be preserved, for environmental reasons. Many extant lycopodialean species are robust enough to make potentially excellent fossils, e.g., *Lycopodiella cernuum*, but most of them today grow far from suitable depositional settings for preservation, certainly more the case than for selaginellaleans.

LEPIDODENDRALEANS CONTINUED:
ISOETALEAN(?) LINE

Included in this section are a number of the squatter herbaceous forms, ranging from *Nathorstianella*, which we might equally have included with the subarborescent lepidodendraleans, to forms so similar to *Isoetes* that they could be accommodated in a slightly enlarged circumscription of that genus. As indicated previously, certain, if not all, species of the Triassic genus *Pleuromeia* could have been included here in the sense that they were herbaceous to suffrutescent.

The earliest Mesozoic records of *Isoetes*-like plants are of *Isoetes* (*Yorkia*) *gramineus* (Ward) Bock (1962, 1969) from the late Triassic of Pennsylvania. Although widely accepted in the literature, Bock provided no convincingly illustrated evidence that these intriguing fossils are like *Isoetes*. Our investigations of the original specimen, re-illustrated in Figure 10, indicate that it is most likely an osmundaceous fern stem with attached petiole bases, such as that described by Schweitzer (1978) and similar to the rhizome material in Figure 3 of this paper. Most importantly, the tips of the petioles (i.e., Bock's leaves) indicate that pinnate divisions characteristic of fern fronds were attached (Fig. 12 and Schweitzer, 1978: pl. 2, fig. 4, textfig. 12). The attachment of these upper regions was not clear in the specimen until a fragment of rock was found in the drawer, which fit between the base and the divided tips. Once this was replaced on the specimen (Fig. 11), the attachment of the alternately divided tips of the petioles (leaves) to the rhizome base became clear. The high angle spiral of attachment of the appendages in Bock's (1962) textfigure A:B and our Figure 13 is more suggestive of a fern stem than a lycopsid shoot, and the broad scaly bases of the petioles are exactly like those described by Schweitzer for *Todites* stems. Furthermore, there is strong evidence that the petiole bases are stipulate (Fig. 13) and that the wiry roots extend away from the rhizome.

This leaves other material figured by Bock (1969) that may well be lycopsid but is certainly not of *Isoetes*-like form: his *Isoetodendron striata* and *Triletes isoetodendron*. *Isoetites circularis* (Emmons) Brown from the Triassic of North Carolina (Brown, 1958) also is untenable as an *Isoetes*-like plant, although it too is probably a lycopsid and further research is clearly needed.

With the possible exception of the poorly dated Indian material referred to below, records from the Jurassic are also unconvincing. They include the type species of the genus *Isoetites*, the aptly named *I. crociformis* Münster, from Daiting in Bavaria (Münster, 1842; Fig. 14). Apart from a superficial similarity to *Isoetes* its affinities are entirely unknown, and it may well represent something similar to a *Czekanowskia* short shoot. Should any reader know of the existence of Münster's material, C. Hill would like to know its location, as it clearly
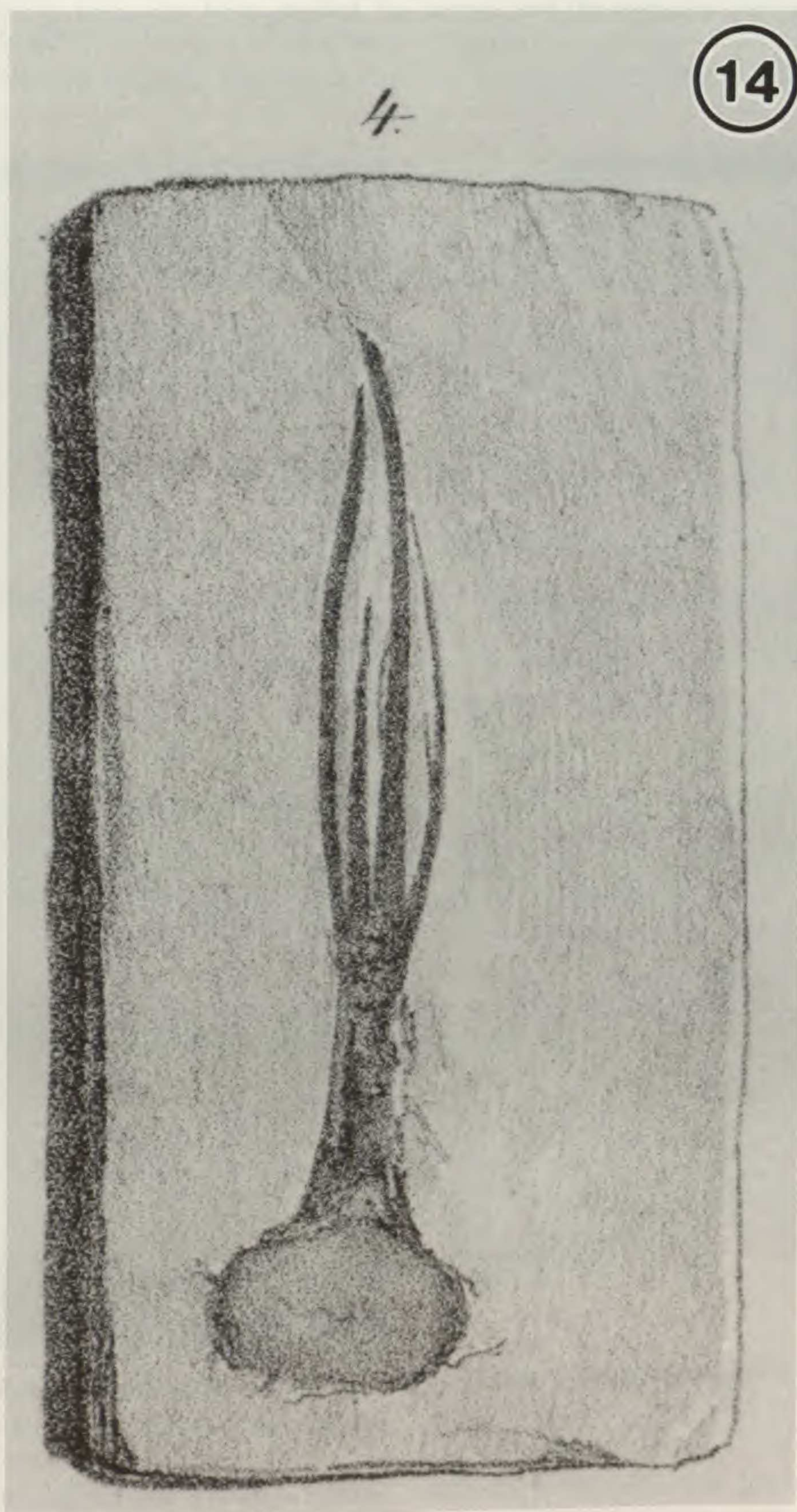
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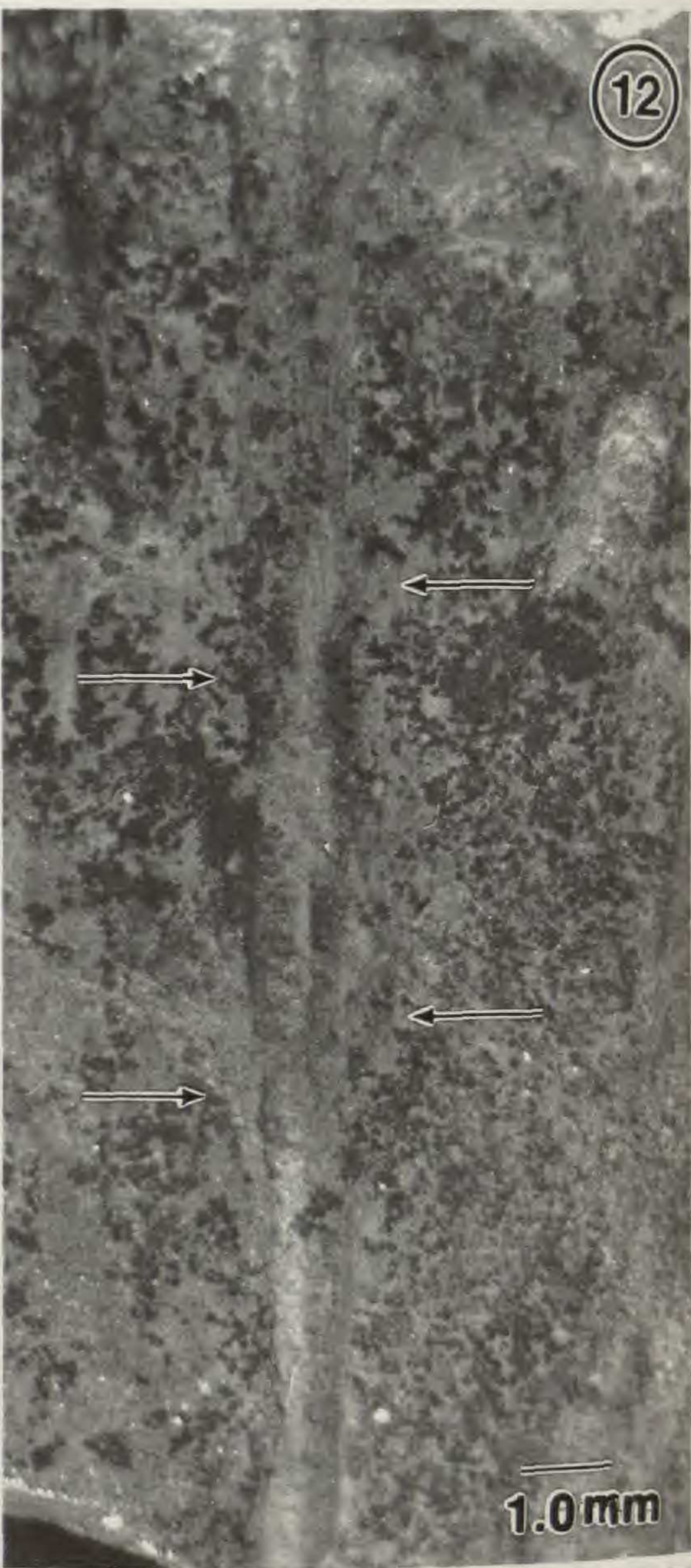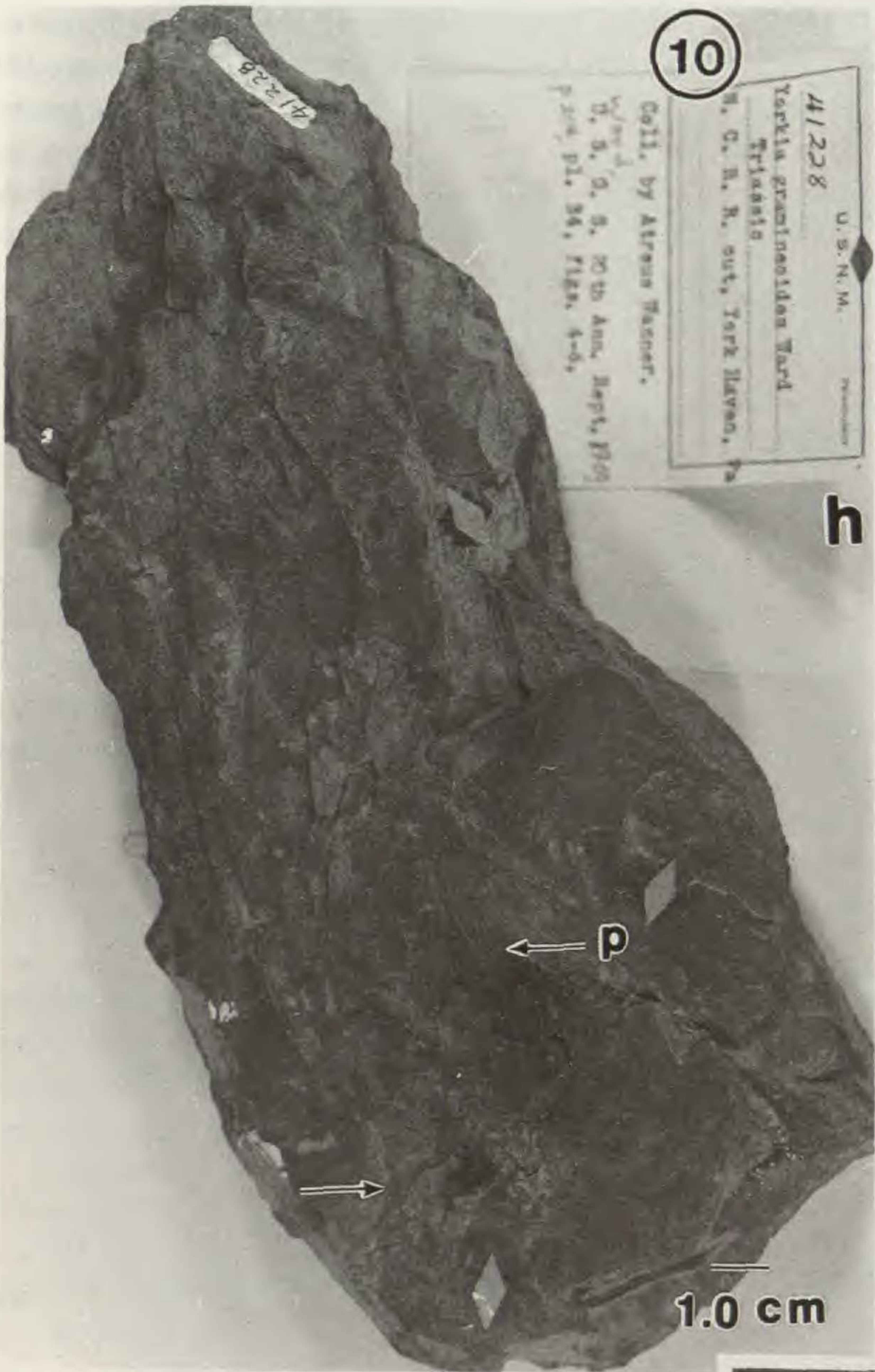
FIGURE 14. *Isoetes crociformis* Münster (1842), Tafel IV, figure 4, shown here at 2.25 × the original illustration.

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FIGURES 10–13. *Yorkia gramineoides* Ward.—10. Holotype specimen USNM 41228 showing rhizome at arrow with elongate petioles (p) extending upward from it.—11. Enlarged portion of Figure 10 showing broken piece at arrow that was replaced from the drawer. Connections of the petioles above and the rhizome below can now be seen.—12. Upper portions of the petioles with pinnate side divisions at arrows. The lower left is the clearest.—13. Enlarged basal rhizome portion of Figure 10 showing the stipules (s), roots (r), and petioles (large arrows).
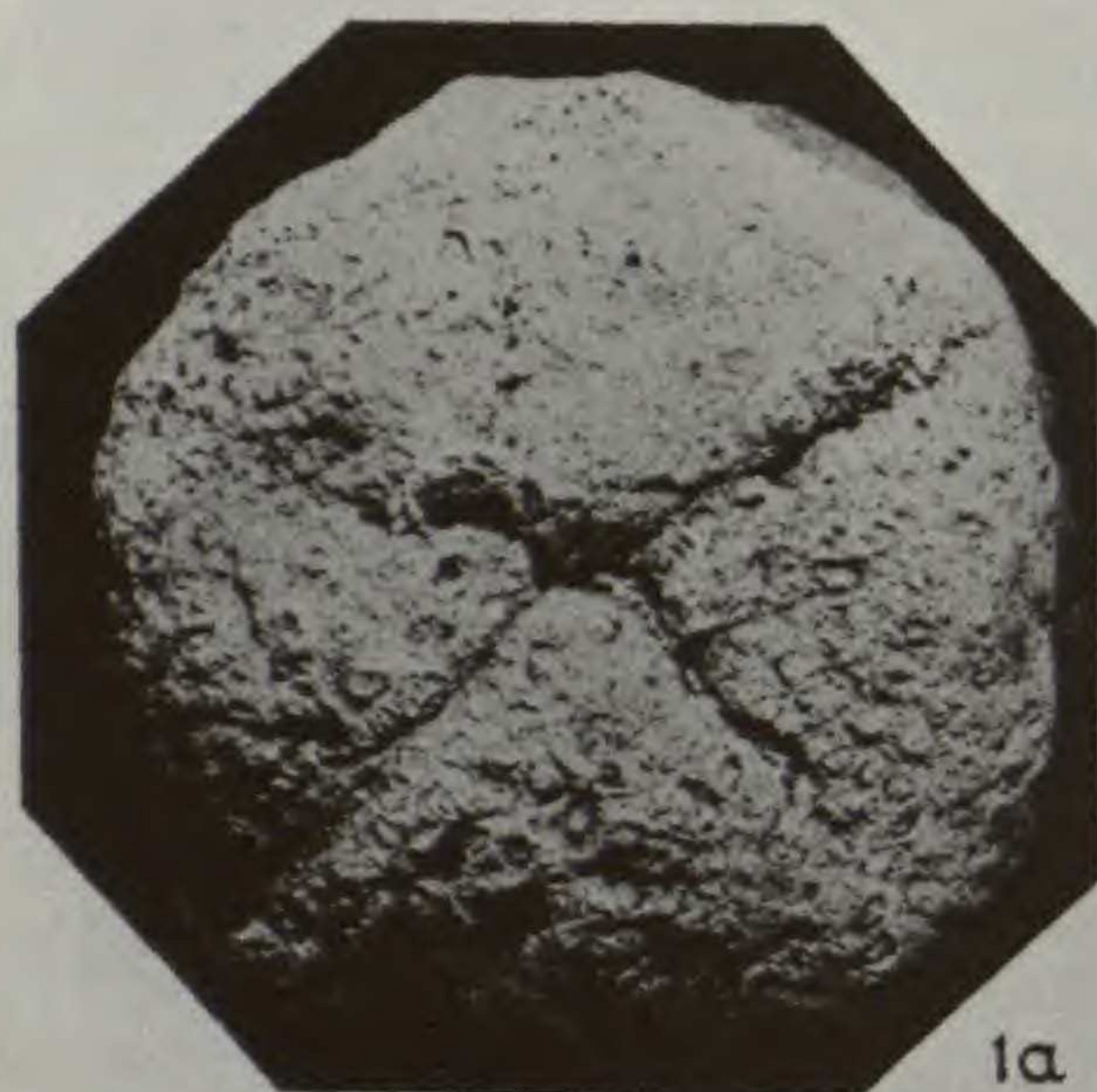
FIGURE 15. *Nathorstianella* Glaessner & Rao, original illustrations from Transactions Royal Society South Australia, 78, plate XI, 1955.

deserves proper study, and adequate typification of the genus depends on this.

This unsatisfactory situation changes dramatically in the early Cretaceous, when good *Isoetes*-like forms appear in force in the fossil record from both hemispheres. The largest and least like *Isoetes*, with elongate stems, are those named *Nathorstianella* from South Australia (Glaessner & Rao, 1955; Fig. 15). The stems were substantial, known from fragments 3–18 cm long and up to 7 cm wide. The slightly expanded basal region bore rootlet scars and was divided into four lobes, while the erect part shows numerous closely crowded leaf base scars with a pattern of annular banding, which may reflect alternating periods of differential growth. Although no leaves or sporophylls are known from South Australia, Walkom (1944) described a crown of elongate tapering sporophylls from the Cretaceous of western Australia, each sporophyll up to 12 cm or longer. At their bases they have either well-preserved megasporangia (with in situ spores preserved) or presumed microsporangia. To our

knowledge the spores have not been studied in detail. Glaessner & Rao (1955) indicated that sporophylls like Walkom's may have been borne on *Nathorstianella* stems, and this may be correct. However, as will be evident from the following, records of Cretaceous *Isoetes*-like stems are now sufficiently diverse to suggest that other forms of stem are equally possible candidates. Conversely, in the absence of attached sporophylls, *Nathorstianella* may represent persistence into the Cretaceous of subarborescent plants such as *Cylostrobus*.

Limnoniobe insignis Krassilov from the early Cretaceous of Mongolia is represented by stem fragments up to 5 cm or more long and 3 cm wide. The stem surface has similar features to *Nathorstianella*, including apparent differential growth increments and it shows both root and sporophyll scars that have a single vascular strand. The sporophylls were more than 7 cm long, were clearly trabeculate, and have *Isoetes*-like epidermal features. Details of attachment of the sporangia are obscure. The large megaspores, however, are well preserved and appear to be referable to the dispersed spore genus *Minerisporites*; they have a very broad zona and relatively subdued acrolamellae. Microspores occur adherent to the megaspores and appear to be monolete (Krassilov, 1982).

Limnoniobe was about the same height as the inaptly named *Nathorstiana arborea* Richter, described by Mägdefrau (1932), the entire plant of which reached up to 10 cm in length with leaves about 5 cm long. Sporangia and spores are unknown. The root-bearing bases were somewhat swollen and were marked by longitudinal furrows. Karrfalt's (1984) detailed study of the stems suggested that the basal swelling may be more apparent than real, resulting from decortication above the base. He detected a developmental sequence from radial (juvenile) through bilateral two-lobed to quadrangular four-lobed forms.

Isoetites choffatii (Figs. 16–19) from the Aptian–Albian of Cercal, Portugal, has been illustrated by Saporta (1894) and Teixeira (1948). Certain specimens named *Delgadopsis rhizostigma* Saporta probably represent more mature material of the same species. The following summary is based partly on material in the paleontological collections of the Natural History Museum, London.

The stems of *Isoetites choffatii* were radial in end view and also appear rounded in lateral view, narrowing upward to a stem about 1 cm wide of unknown length. The bulbous base bears abundant roots, and the stem has numerous crowded scars of attachment, apparently of sporophylls. The overall appearance of these stem bases resembles that of the Paleozoic genus *Cormophyton* and, equally, is not unlike the base of *Nathorstiana* but lacks vertical ribs and displays no evidence of stem decortication or lobing; however, there is a hint of bilateral symmetry. The associated sporophylls are small, 2–3 cm long, with a pointed lamina; they are trabeculate and of typical *Isoetes*-like form. Compressed megaspores are preserved both in situ and closely associated with the sporophylls, but their detailed morphology has yet to be examined.

Specimens from the early Cretaceous of Victoria referred to *Isoetes bulbiformis* by Drinnan & Chambers (1986) are probably pentoxylalean fertile short shoots (A. Rozefelds, pers. comm.). There is no detailed evidence that they represent *Isoetes*-like fossils.

All of the Cretaceous species discussed so far had more or less elongate stems; some, such as *Nathorstianella* and *Limnoniobe*, were rather longer and wider than their nearest extant analogues such as *Isoetes andicola*, the others were apparently well within or matching the size limits of extant species. Since no widely ranging studies have been made of the form of stems of extant species stripped of their appendages at various stages of development and decortication, it is difficult to compare the fossil stems with those of extant species or vice versa.

For the remaining Cretaceous species there is direct evidence that their stems were "corm"-like as in many extant species, or else their preservation as compact crowns without stems suggests indirectly that the stems were cormose.

Isoetites sp. nov. C. Hill (Figs. 20–30) from the Cretaceous of southeastern England is preserved as permineralized crowns, some of which are borne on a small, essentially bilobed corm (not illustrated here) bearing poorly preserved root scars. Only the bases of the sporophylls are preserved in the crowns, but because they are up to 7 cm long, this suggests that the original length of the complete sporophylls was considerably longer, perhaps up to 15–30 cm. The sporophylls were rounded or angular in section, trabeculate, with typically *Isoetes*-like epidermal cells (Fig. 26). Their expanded bases were ligulate and apparently had a velum partly covering the oval sporangia. These were trabeculate, large (about 8–13 mm long by 3–5 mm wide). They yield either many thousands of monolete microspores (Fig. 30) or several hundred trilete, rounded to subangular megaspores (Figs. 27–29) about 425 × 450 μm
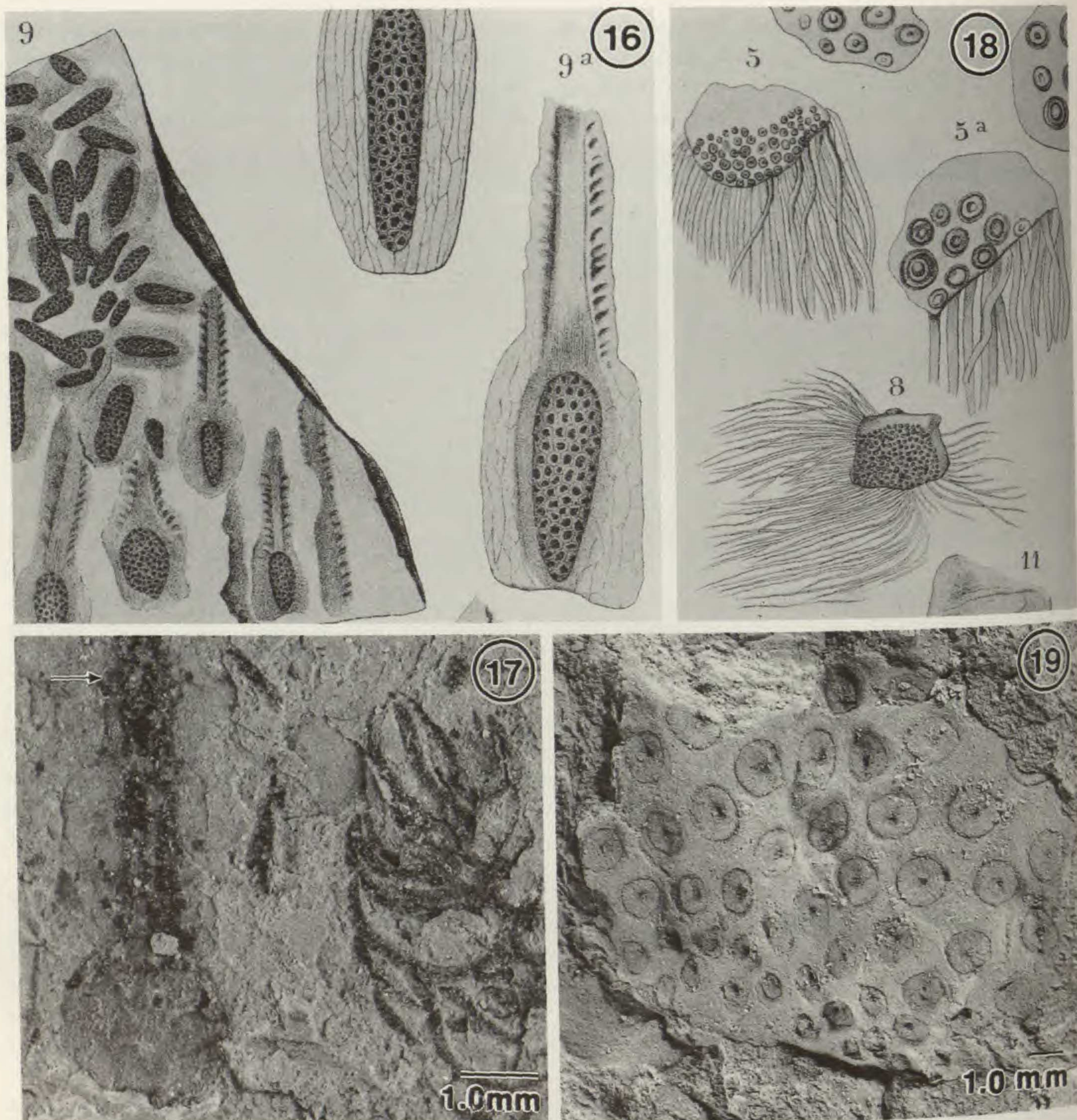
FIGURES 16–19. *Isoetes choffatii* Saporta. Figures 16, 17. Sporophylls.—16. Selected drawings reproduced from Saporta (1894), plate XXIV, figure 9 at natural size, the other figures being enlargements showing evident cellular details and spores.—17. At left of photo, an actual sporophyll base from Cercal, with a few adherent megaspores (one of which is at arrow), at right a *Lycopodites* shoot, v. 23601. 18, 19. Corms with rootlets and rootlet scars.—18. Selected drawings reproduced from Saporta (1894), plate XXV, figures 5 and 8 at natural size, the others enlarged.—19. An actual corm from Cercal with rootlet scars, v. 23596, collected by W. N. Edwards in 1934.

wide in polar view. The megaspores are zonate, of *Minerisporites* form with rather subdued acrolamellae; their sculpture is reticulate, normally of low muri bearing spines; they are not attributable to any described dispersed species known to us.

This *Isoetites* compares favorably in its general morphology with several extant tropical lacustrine species. It differs from all extant species, however, in having a larger megaspore productivity per sporangium, and, to the extent that knowledge of

FIGURES 20–25. *Isoetes* sp. nov. C. Hill. All scale bars = 1 cm.—20. v. 63454, side view.—21. v. 63456, basal view showing corm.—22. v. 63454, longitudinal medial section of Figure 20.—23. v. 63455, side view showing sporophyll lamina impression, as longitudinal furrow.—24. v. 63458, basal view showing ring of fertile basal regions of sporophylls.—25. v. 63459, transverse section.
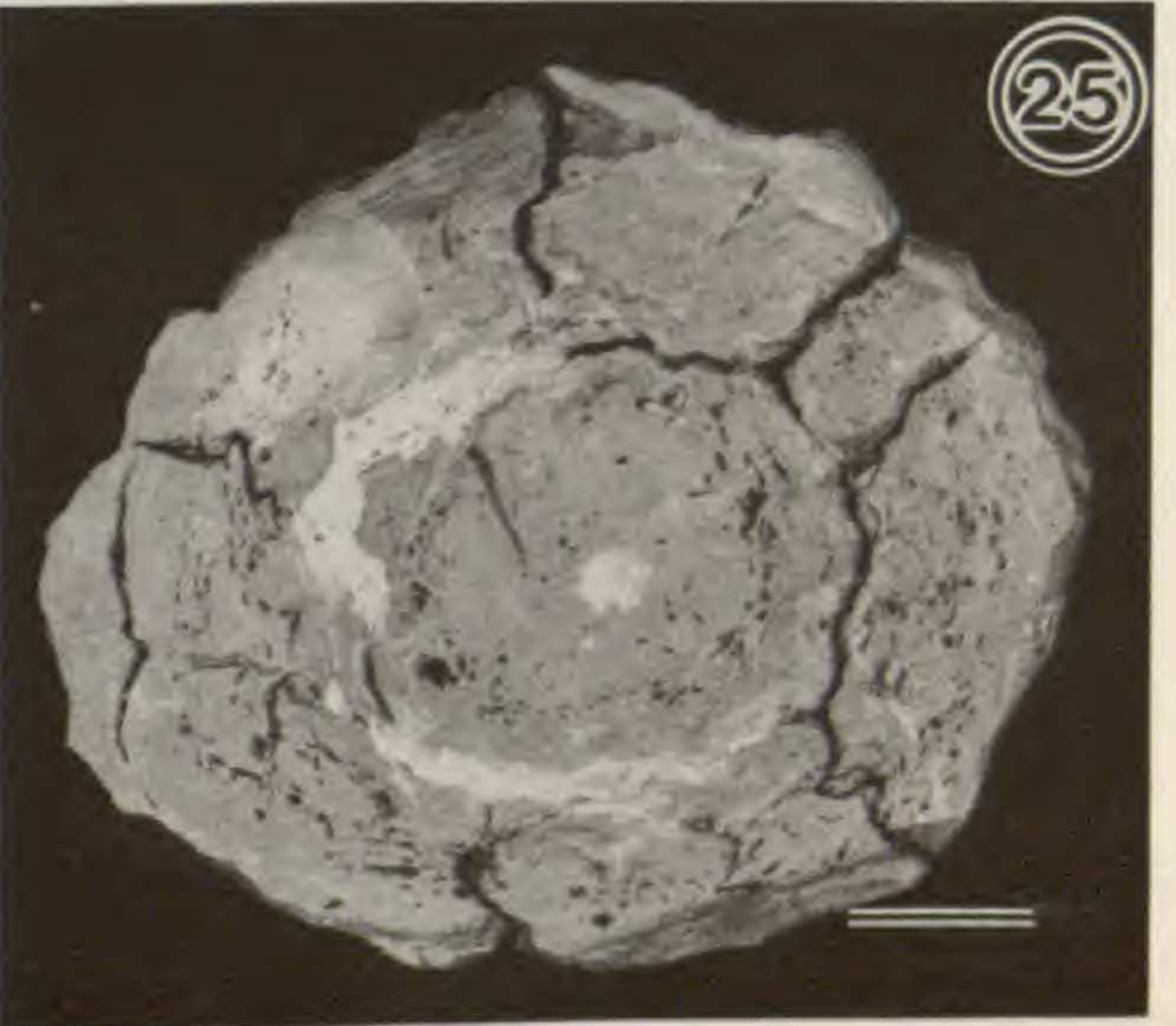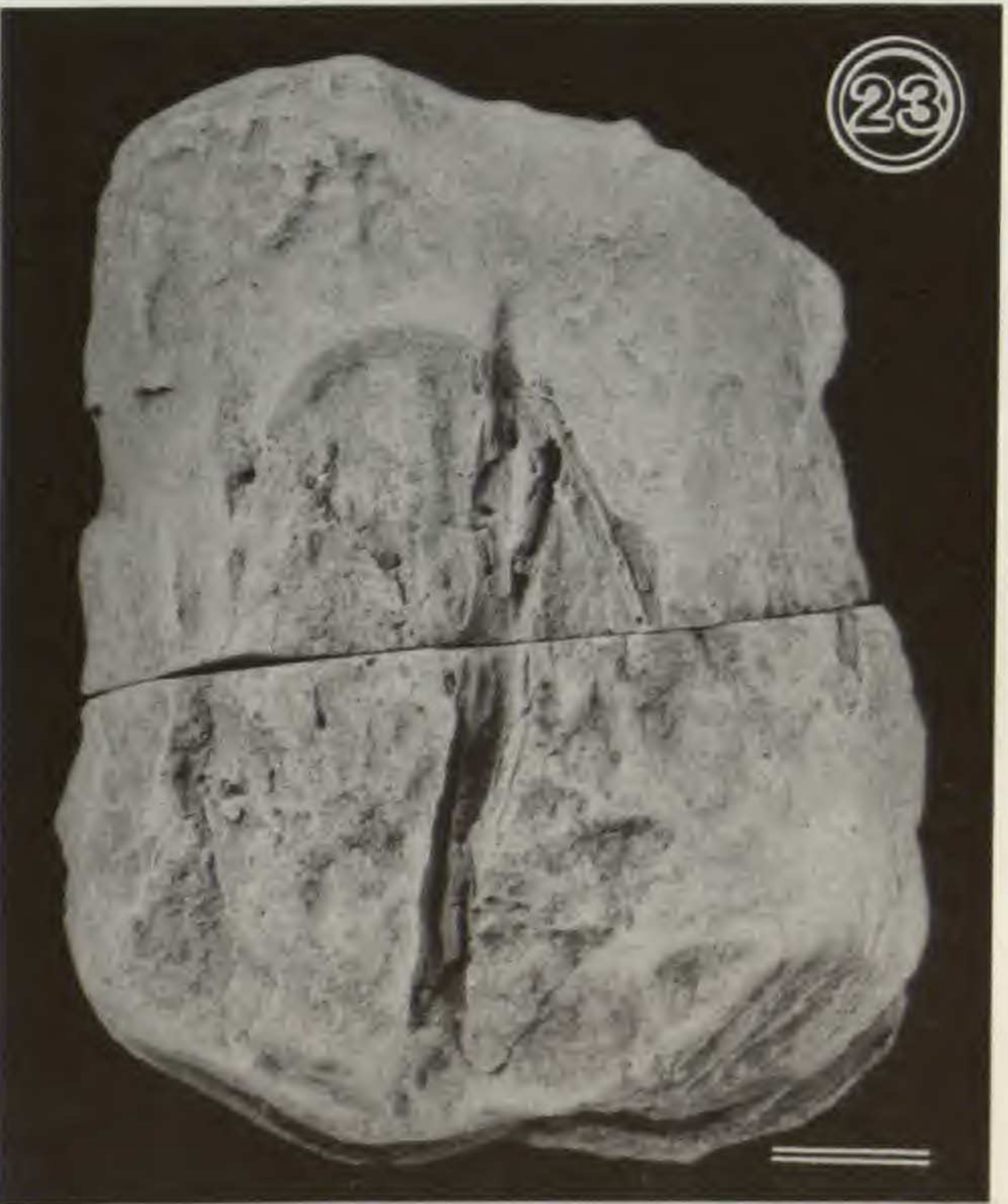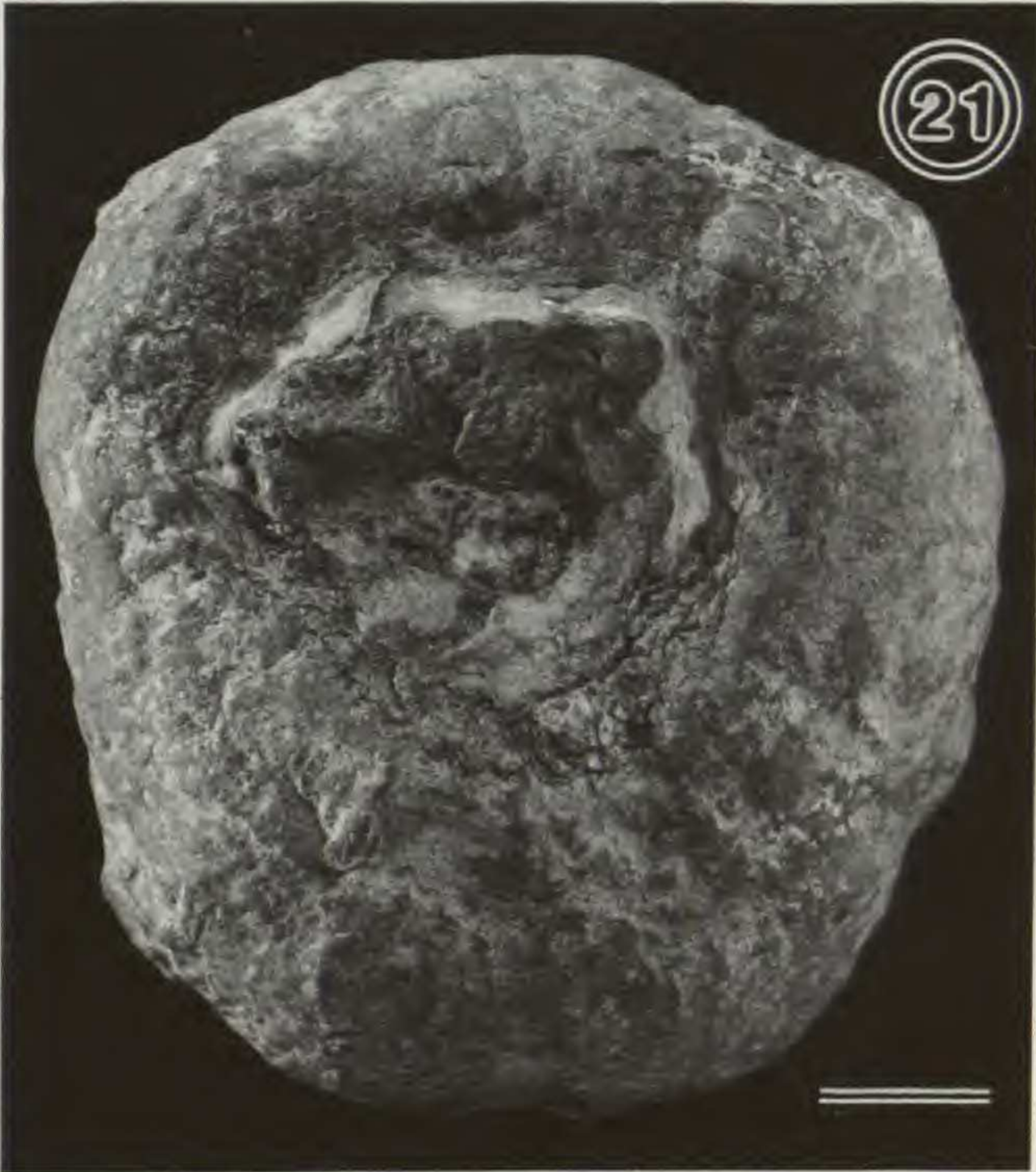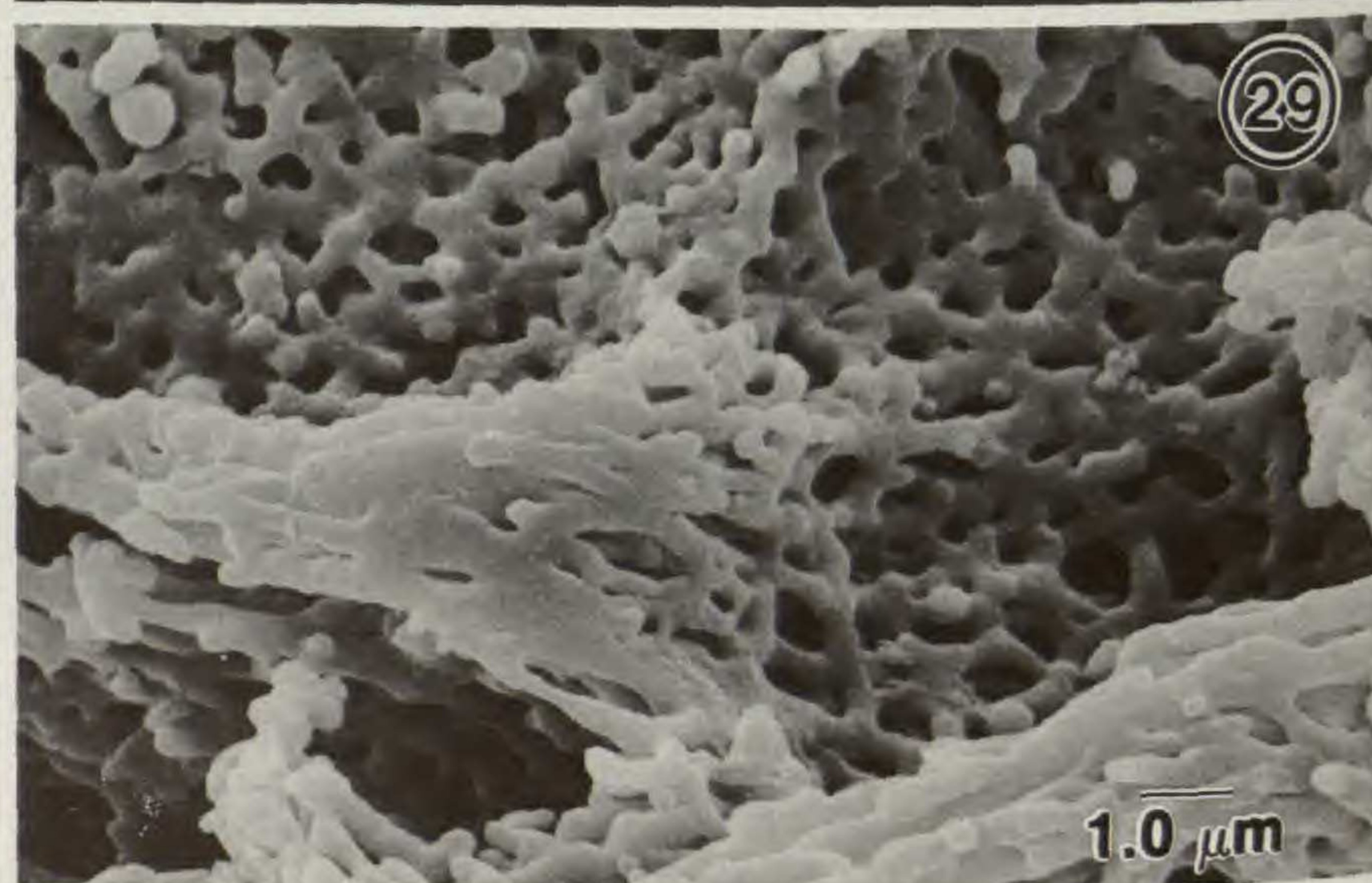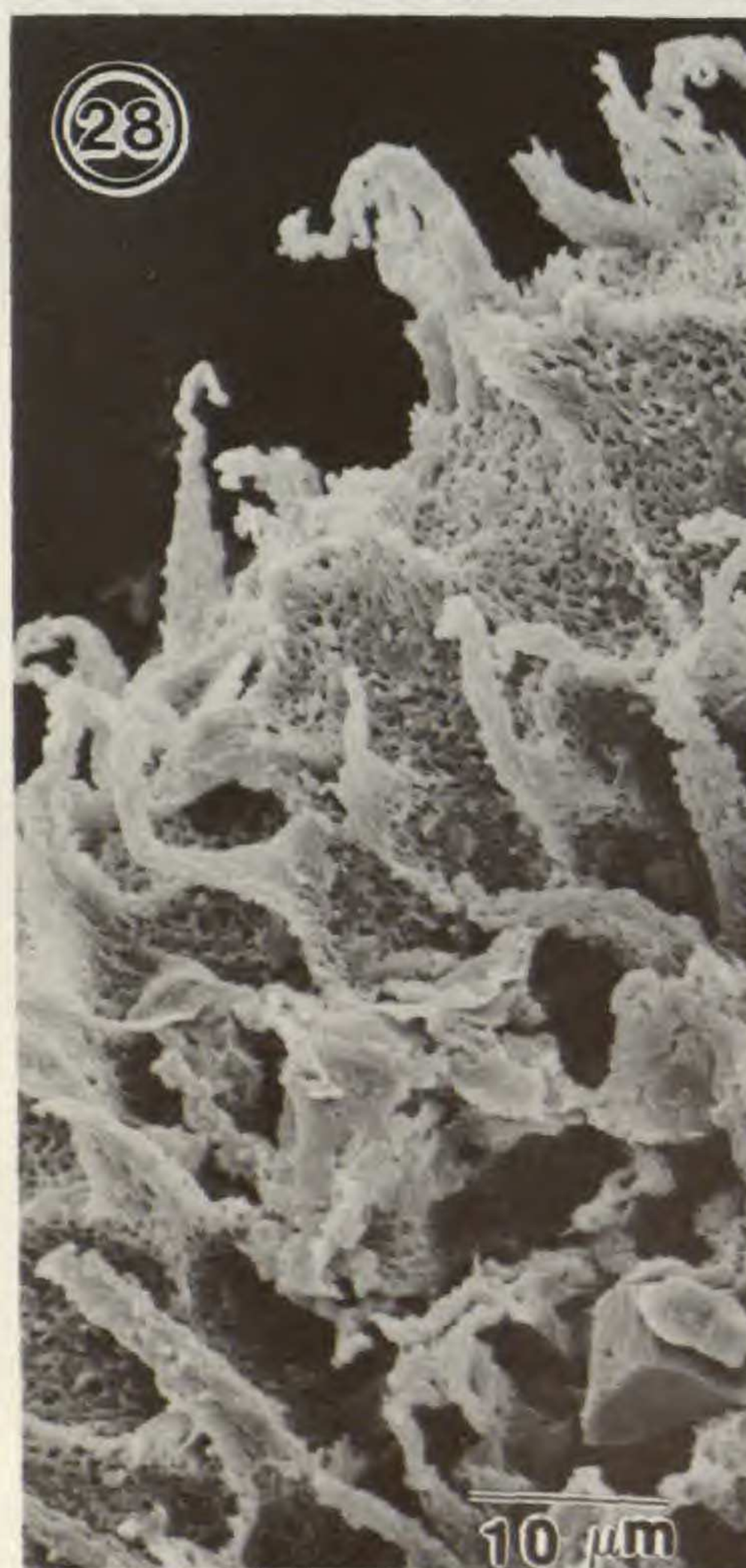
corms of extant species permits comparison, the aerial apex of the corm in the fossil is more elongated, so that it appears more acutely conical in section. To the extent that the spores can be compared, the fossil ones also resemble those of some extant species.

A comparable species to the British *Isoetites* is *Isoetes janaianus* Banerji, previously described as *Isoetites indicus* Bose & Roy (1964) from the ?middle to late Jurassic (Banerji, 1989) to (more likely) early Cretaceous of northwestern India (see also Bose & Banerji, 1984; Sukh-Dev, 1980). Although it has a five-lobed corm and is smaller than the British material, it is otherwise very similar. It too has yielded megaspores of *Minerisporites* form produced in large numbers (Bose and Roy estimated more than 1,500 per megasporangium; Banerji, 1989, reported 100–1,500). The most comparable dispersed megaspores appear to be *Minerisporites cutchensis* and *M. auriculatus* (Banerji et al., 1984; Sukh-Dev, 1980). These have a fine reticulum like the in situ spores of *Isoetes janaianus* and similar to the spores of the British fossil.

A coeval *Isoetites* species from India is *I. serratifolius* Bose & Roy (see also Bose & Banerji, 1984 who provide a partial reconstruction of the parent plant). It has large, well-preserved laminate sporophylls up to 1.5 cm wide that had serrate margins to the distal region beyond their expanded bases. Such margins are unknown in any extant species. Unfortunately, no material has yet been found with in situ spores, and this material is known only from detached sporophylls (Bose & Roy, 1964). The sporangia were large, up to 12 mm long. The basal parts of the sporophylls have a remarkably similar outline to those of Triassic lepidodendraleans such as *Skilliostrobus* and certain species currently referred to *Tomiostrobus*.

A distinctive pair of *Isoetites* species that also had serrate sporophylls is known from the late Cretaceous to early Tertiary of North America. However, these were even less like extant *Isoetes* than the Indian material just mentioned. In the Upper Cretaceous *Isoetites serratus* Brown (1939, 1958), the strongly trabeculate sporophylls not only had minutely serrate distal margins but were

also markedly spatulate distally. Collinson (1988, 1992) drew attention to the possibility that the spatulate distal regions of the sporophylls in this and especially the next species were dehiscent—quite unlike extant *Isoetes*. Other characters of *I. serratus* were similar to those of extinct species and extant *Isoetes*; for example, although a corm is not known preserved, the sporophylls were evidently disposed around a corm to form a crown and they had typical epidermal cells apparently without stomata.

Isoetites horridus (Dawson) Brown (see also Melchior, 1977 and Hickey, 1977) from the late Cretaceous to Eocene of North America also had markedly trabeculate and distally expanded sporophylls Brown (1939, 1958). It is thus similar morphologically to *I. serratus*, although the sporophyll margins are entire and a corm or short stem is preserved. In situ spores have been well described and illustrated by Hickey (1977) and Melchior (1977), who attributed them to the dispersed spore species *Minerisporites mirabilis* (Miner) Potonié. This North American material requires fresh study using modern techniques.

Since we have now digressed into the early Tertiary, we should mention the record of sporophylls with ?*Minerisporites* megaspores from the Oligocene to Miocene of Tasmania, named *Isoetes reticulata* by R. S. Hill (1987).

SUMMARY: ISOETALEANS

These records of Mesozoic and early Tertiary *Isoetes*-like forms encompass several species that, at least in principle, may be related to groups of species within the extant genus. Others extend the range of form of *Isoetes* to greater or lesser extent. Although knowledge of these fossils is growing rapidly, it is clear that much further, carefully focussed work needs to be done on them and on extant species if comparisons are to be effective.

Environmentally, the evidence is slim but suggests that these forms have always occupied the same niches as their living descendants. Apart from the indirect evidence supplied by megaspores (noted previously), the rarity of the megafossils suggests that they were not immediate occupants of the high-energy fluvial environments of deposition fa-

FIGURES 26–30. *Isoetes* sp. nov. C. Hill.—26. v. 63455, surface details indicating cell outlines.—27. v. 63455, SEM of trilete megaspore, proximal view.—28. v. 63455, SEM enlarged of Figure 27 showing ornamentation of spines.—29. v. 63455, SEM enlarged showing reticulate pattern of exine below ornamentation.—30. v. 63457, SEM of cluster of microspores.

vored in the sedimentary record of plants, but that they grew instead in associated low-energy lacustrine and marsh settings. Although there is no absolute correlation even among extant species (Thomas & Masarati, 1982), the apparent lack of stomata from any of the fossil sporophylls so far known suggests that the plants we know as megafossils were growing more or less submerged in water as lacustrine forms; this makes sense in terms of sedimentological bias and should not be taken as evidence that there were no species growing coevally in more exposed marshy environments. Indeed, it is these that are likely to be represented indirectly, by those megaspores that cannot be linked to megafossils. At present the lacustrine species are virtually cosmopolitan in distribution, but those of larger size comparable to *Isoetites* sp. nov. are mainly tropical; on uniformitarian grounds this indicates that Cretaceous lowland Britain was likely to have been warm and, despite many other indicators of widespread seasonally moderately arid or salt-stressed conditions, was at least locally sufficiently wet to sustain shallow freshwater lakes.

Phylogeny

Any account of Mesozoic lycopsid phylogeny cannot adequately be divorced from an understanding of lycopsid relationships as a whole. This must be based on detailed knowledge of extant as well as of extinct forms, including extinct plants from as far back as the Devonian in geologic time, as is obvious from the papers in this collection. Hence, our treatment here of wider aspects is brief and provisional. Some of the main points of interest are as follows.

(1) As was recognized by Townrow (1968), *Selaginella harrisiana* possessed many derived characters but it retained several generalized characters in its evidently leafless rhizome, which thus resembled the rhizomes of more plesiomorphous lycopsids. This is of considerable value in indicating the likely generalized condition of the main rooting system in *Selaginella* as a whole.

(2) The apparently rather confusing admixture of characters in Mesozoic *Lycopodites* species such as *L. macrostomus* and *L. falcatus* can be reconciled if related to the selaginellaleans. Thus, for instance, *L. macrostomus*, while vegetatively *Huperzia*-like, had apparently ligulate leaves. Several such extinct species may have retained many "lycopodialean" features together with a few "selaginellalean" ones, in contrast to those at the other end of this apparently paraphyletic spectrum of forms, such as *Selaginella harrisiana*, which re-

tained just a few "lycopodialean" features. To that extent, when interpreted in a cladistic sense, these forms are "selaginellalean" rather than "lycopodialean." In this light it may not be surprising if either *Lycopodites macrostomus* or *L. falcatus* prove to be heterosporous. These Mesozoic species appear to provide hitherto unrecognized evidence, albeit tentative, of links and/or homoplasies between the extant selaginellaleans and lycopodialeans that may call into question their apparent monophyly as represented by the surviving species.

(3) A growing number of accurately identified *Isoetes*-like forms is becoming better known. Together with permineralized Mesozoic specimens of such genera as *Pleuromeia* and in particular *Takhtajanodoxa* (Snigirevskaya, 1980), this provides a promising basis for improved comparison with Paleozoic material, and this, in turn, is leading to greater clarity in our present understanding of the origin of *Isoetes*.

Summary

Following the extinctions of the Paleozoic lycopsids, the Mesozoic is perceived as a time of comparative silence regarding the evolution of this major group of plants. Yet when the record is critically examined there is evidence of diversity among the now mainly herbaceous lycopsids. The three main lines that have continued into the Recent (Isoetales, Selaginellales, and Lycopodiales) are well established within various habitats. Problems arise because of the scarcity of known megafossils, specimens that are poorly known, confusion between the lycopsids and other groups of plants when not enough characters can be seen (gymnosperms and bryophytes in particular as Seward noted in 1910), and difficulty in correlations between the palynological and megafossil records. In this paper we have tried to summarize the state of knowledge for the Mesozoic lycopsids, to indicate trends of evolution that may have been occurring during this time interval, to offer some new information on lycopsids represented as megafossils, and especially to suggest some critical areas for future research.

Literature Cited

ASH, S. 1972. Late Triassic plants from the Chinle Formation in north-eastern Arizona. Palaeontology 15: 598–618.

———. 1979. *Skilliostrobus* gen. nov., a new lycopsid cone from the Early Triassic of Australia. Alcheringa 3: 73–89.

BANERJI, J. 1989. Some Mesozoic plant remains from Bhuj Formation with remarks on the depositional environment of beds. Palaeobotanist 37: 159–168.

——, B. N. JAHA & H. K. MAHESHWARI. 1984. The fossil floras of Kachchh. II. Mesozoic megaspores. Palaeobotanist 33: 190–227.

BATTEN, D. J. 1988. Revision of S. J. Dijkstra's Late Cretaceous megaspores and other plant microfossils from Limburg, The Netherlands. Meded. Rijks Geol. Dienst 41(3): 1–55.

—— & W. L. KOVACH. 1990. Catalog of Mesozoic and Tertiary Megaspores. AASP Contributions 24.

BERRY, E. W. 1910. A Cretaceous *Lycopodium*. Amer. J. Sci. 30: 275–276.

BLACK, M. 1934a. III. The Middle Jurassic rocks. Proc. Geol. Assoc. 45: 261–274.

——. 1934b. Sedimentation of the Aalenian rocks of Yorkshire. Proc. Yorkshire Geol. Soc. 22: 265–279.

BOCK, W. 1962. A study of fossil *Isoetes*. J. Paleontology 36: 53–59.

——. 1969. The American Triassic flora and global distribution. Geological Center Research Series 3 and 4: 1–406.

BOSE, M. N. & J. BANERJI. 1984. The fossil floras of Kachchh. I—Mesozoic megafossils. Palaeobotanist 33: 1–189.

—— & S. K. ROY. 1964. Studies on the Upper Gondwana of Kutch. 2. Isoetaceae. Palaeobotanist 12: 226–228.

BROWN, R. W. 1939. Some American fossil plants belonging to the Isoetales. J. Wash. Acad. Sci. 29: 261–269.

——. 1958. New occurrences of the fossil quillworts called *Isoetites*. J. Wash. Acad. Sci. 48: 358–361.

CHALONER, W. & E. BOUREAU. 1967. Lycophyta. Pp. 435–802 in E. Boureau (editor), Traité de Paléobotanique. Tome II Bryophyta, Psilophyta, Lycophyta. Masson & Cie., Paris.

—— & S. TURNER. 1987. An enigmatic Triassic lycopod axis from Australia. Rev. Palaeobot. Palynol. 51: 51–58.

COLLINSON, M. E. 1988. Freshwater macrophytes in palaeolimnology. Palaeogeog. Palaeoclimatol. Palaeoecol. 62: 317–342.

——. 1992. Diversification of modern heterosporous pteridophytes. In: S. Blackmore & S. Barnes (editors), Pollen and Spores: Patterns of Diversification. Syst. Assoc. Spec. Vol. 44: 119–150. Clarendon Press, Oxford.

COOKSON, I. C. & M. E. DETTMAN. 1958. Some trilete spores from Upper Mesozoic deposits in the eastern Australian region. Proc. Roy. Soc. Victoria 70: 95–128.

COUPER, R. A. 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zealand Geol. Surv. Palaeontol. Bull. 22: 1–179.

DAUGHERTY, L. H. 1941. The Upper Triassic flora of Arizona, with a discussion of its geologic occurrence by H. R. Stagner. Publication No. 526, Carnegie Institution of Washington, Washington, D.C.

DAVIS, P. H. & V. H. HEYWOOD. 1963. Principles of Angiosperm Taxonomy. Van Nostrand, Princeton, New Jersey.

DETTMAN, M. E. 1963. Upper Mesozoic microfloras from southeastern Australia. Proc. Roy. Soc. Victoria 77: 1–148.

DOBRUSKINA, I. A. 1974. Triassic lepidophytes. Paleontological J. 8: 384–397.

DRINNAN, A. & S. CHAMBERS. 1986. Floras of the Lower

Cretaceous Koonwarra Fossil Bed (Korumburra Group) South Gippsland, Victoria. In: P. A. Jell & J. Roberts (editors), Plants and Invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria. Assoc. Australasian Palaeontol. Sydney Mem. 3: 20–23.

EDWARDS, W. N. 1934. Jurassic plants from New Zealand. Ann. Mag. Nat. Hist. 13: 81–109, pls. 4, 5.

FRIIS, E. M. & K. R. PEDERSEN. 1990. Structure of the Lower Cretaceous fern *Onychiopsis psilotoides* from Bornholm, Denmark. Rev. Palaeobot. Palynol. 66: 47–63.

FUGLEWICZ, R. 1980. Stratigraphy and palaeogeography of the Lower Triassic in Poland on the basis of megaspores. Acta Geol. Polonica 30: 417–470.

GLAESSNER, M. F. & V. R. RAO. 1955. Lower Cretaceous plant remains from the vicinity of Mount Babbage, South Australia. Trans. Roy. Soc. South Australia 78: 134–140.

GRAUVOGEL-STAMM, L. & P. DURINGER. 1983. *Annalepis zeilleri* Fliche 1910 emend., un organe reproducteur de Lycophyte de la Lettenkohle de l'Est de la France. Morphologie, spores in situ et paléoécologie. Geol. Rundschau 72: 23–51.

GRIERSON, J. D. & P. M. BONAMO. 1979. *Leclercqia complexa*: earliest ligulate lycopod (Middle Devonian). Amer. J. Bot. 66: 474–476.

HARRIS, T. M. 1935. The fossil flora of Scoresby Sound, East Greenland. Part 4: Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. Meddel. Grønland 112: 1–176.

——. 1961. The Yorkshire Jurassic Flora, I: Thallophyta–Pteridophyta. British Museum (Natural History), London.

——. 1976. A slender upright plant from Wealden sandstones. Proc. Geol. Assoc. 87: 413–422.

——. 1979. The Yorkshire Jurassic Flora, 5: Coniferales. British Museum (Natural History.) London.

HELBY, R. A. & A. R. H. MARTIN. 1965. *Cylostrobus* gen. nov., cones of lycopsidean plants from the Narrabeen Group (Triassic) of New South Wales. Austral. J. Bot. 13: 389–404.

HICKEY, L. J. 1977. Stratigraphy and Paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Mem. No. 150, Geol. Soc. Amer., Boulder, Colorado.

HICKEY, R. J. 1986a. *Isoetes* megaspore surface morphology: nomenclature, variation, and systematic importance. Amer. Fern J. 76: 1–16.

——. 1986b. The early evolutionary and morphological diversity of *Isoetes*, with descriptions of two new neotropical species. Syst. Bot. 11(2): 309–321.

——, W. C. TAYLOR & N. T. LUEBKE. 1989. The species concept in pteridophyta with special reference to *Isoetes*. Amer. Fern J. 79: 78–89.

HILL, C. R. & P. CRANE. 1982. Evolutionary cladistics and the origin of angiosperms. Pp. 269–361 in K. A. Joysey & A. E. Friday (editors), Problems of Phylogenetic Reconstruction. Academic Press, London.

——, D. T. MOORE, J. T. GREENSMITH & R. WILLIAMS. 1985. Palaeobotany and petrology of a Middle Jurassic ironstone bed at Wrack Hills, North Yorkshire. Proc. Yorkshire Geol. Soc. 45: 277–292.

HILL, R. S. 1987. Tertiary *Isoetes* from Tasmania. Alcheringa 12: 157–162.

HORST, U. 1954. Merkwürdige Gebilde in kohlem aus dem Wealden. Geologie 3: 610–612.

HUEBER, F. M. 1982. Megaspores and a palynomorph from the Lower Potomac Group in Virginia. Smithsonian Contr. Paleobiol. 49: 1–69.

HUGHES, N. F. 1955. Wealden plant microfossils. Geol. Mag. 92: 201–217.

KARRFALT, E. 1981. The comparative and developmental morphology of the root system of Selaginella selaginelloides (L.) Link. Amer. J. Bot. 68: 244–253.

———. 1984. Further observations on Nathorstiana (Isoetaceae). Amer. J. Bot. 71: 1023–1030.

KOPPELHUS, E. B. & D. J. BATTEN. 1989. Late Cretaceous megaspores from southern Sweden: morphology and palaeoenvironmental significance. Palynology 13: 91–120.

KOVACH, W. L. 1988. Quantitative palaeoecology of megaspores and other dispersed plant remains from the Cenomanian of Kansas, U.S.A. Cretaceous Res. 9: 265–283.

———. 1989. Quantitative methods for the study of lycopod megaspore ultrastructure. Rev. Palaeobot. Palynol. 57: 233–246.

——— & D. J. BATTEN. 1989. Worldwide stratigraphic occurrences of Mesozoic and Tertiary megaspores. Palynology 13: 247–277.

——— & D. L. DILCHER. 1985. Morphology, ultrastructure, and paleoecology of Paxillitriletes vittatus, sp. nov. from the Mid-Cretaceous (Cenomanian) of Kansas. Palynology 9: 85–94.

——— & ———. 1988. Megaspores and other dispersed plant remains from the Dakota Formation (Cenomanian) of Kansas, U.S.A. Palynology 12: 89–119.

KRASSILOV, V. 1978. Mesozoic lycopods and ferns from the Bureja Basin. Palaeontographica, Abt. B. 166: 16–29.

———. 1982. Early Cretaceous flora of Mongolia. Palaeontographica, Abt. B. 181: 1–43.

LI XING-XUE, YET MEI-RA & AHI-YAN ZHOU. 1986. Late Early Cretaceous flora from Shansong, Jiache, Jalin Province, Northeast China. Palaeont. Cathayana 3: 1–143.

LUNDBLAD, B. 1948. A selaginelloid strobilus from East Greenland (Triassic). Meddel. Dansk. Geol. Forening 11: 351–363.

———. 1950a. On a fossil Selaginella from the Rhaetic of Hyllinge, Scania. Svensk Bot. Tidskr. 44: 477–487.

———. 1950b. Studies in the Rhaeto-Liassic floras of Sweden I. Pteridophyta, Pteridospermae, and Cycadophyta from the mining district of northwest Scania. Kungl. Svenska Vetenskapsakad. Handl. 1: 1–82.

MÄGDEFRAU, K. 1931. Zur Morphologie und phylogenetischen Bedeutung der fossilen Pflanzengattung Pleuromeia. Beih. Bot. Centralbl. 48: 119–140.

———. 1932. Über Nathorstiana, eine Isöetaceae aus dem Neokom von Quedlinburg a. Harz. Beih. Bot. Centralbl. 49: 706–718.

———. 1956. Paläobiologie der Pflanzen. Fischer, Geneva.

MARCINKIEWICZ, T. 1981. Jurassic megaspores from Grojec near Kraków. Acta Palaeobot. 21: 37–60.

MELCHIOR, R. C. 1977. On the occurrence of Minerisporites mirabilis in situ. Sci. Publ. Sci. Mus. Minnesota, new series 3(4): 1–11.

MILLER, C. N. 1968. The lepidophytic affinities of the genus Chinlea and Osmundites walkeri. Amer. J. Bot. 55: 109–115.

MORBELLI, M. A. & B. PETRIELLA. 1973. Austrostrobus ornatum nov. gen. et sp., cono petrificado de Lycopsida del Triasico de Santa Cruz (Argentina). Revista Mus. La Plata, (Nueva Serie) Paleontol. 7: 279–289.

MÜNSTER, G. G. 1842. Beiträge zur Petrefactenkunde. 5: 1–131. Bayreuth.

NATHORST, A. G. 1897. Zur mesozoischen flora Spitzbergens. Kungl. Svenska Vetenskapsakad. Handl. 30: 1–77.

———. 1908. Lycostrobus scotti, eine grosse Sporophyllähre aus den rätischen Ablagerungen Schonens. Kungl. Svenska Vetenskapsakad. Handl. 43: 3–14.

NEUBURG, M. F. 1936. On the stratigraphy of the coal-bearing deposits of the Kuznetsk Basin. Izvestia Akad. Nauk SSSR, Ser. Geol. 4: 455–510.

———. 1960. Pleuromeia Corda from the Lower Triassic shales of the Russian Platform. Trudy Geologicheskogo Instituta. Izvestia Akad. Nauk SSSR 43: 65–94.

ØLLGAARD, B. 1987. A revised classification of the Lycopodiaceae s. lat. Opera Bot. 92: 153–178.

———. 1989. Index of the Lycopodiaceae. Biol. Skr. 34: 1–135.

PAL, P. K. & A. K. GHOSH. 1990. Proposal to conserve Lycopodites Lindley and Hutton against Lycopodites Brongniart (Fossiles). Taxon 39: 129–131.

PANT, D. D. & G. K. SRIVASTAVA. 1962. The genus Isoetes in India. Proc. Natl. Inst. Sci. India, Pt. B, Biol. Sci. 28: 242–280.

PHILLIPS, P. P. & C. J. FELIX. 1971. A study of lower and middle Cretaceous spores and pollen from the southeastern United States. I. Spores. Pollen & Spores 13: 279–348.

POTONIÉ, R. 1956. Synopsis der Gattungen der Sporae Dispersae I Teil: Sporites. Beih. Geologischen Jahrbuch 23.

RETALLACK, G. J. 1975. The life and times of a Triassic lycopod. Alcheringa 1: 3–19.

SADOVNIKOV, G. N. 1982. The morphology, systematics and distribution of the genus Tomiostrobus. Paleontological J. 16: 100–109.

SAPORTA, MARQUIS DE. 1894. Flore Fossile du Portugal. Nouvelles Contributions à la Flore Mesozoïque. Accompagnées d'une Notice Stratigraphique par Paul Choffat. L'Académie Royale des Sciences, Lisbonne.

SCHWEITZER, H. J. 1978. Die Rato-Jurassischen Floren des Iran und Afghanistans. 5. Todites princeps, Thaumatopteris brauniana, und Phlebopteris polypodiodes. Palaeontographica, Abt. B. 168: 17–60.

SCOTT, A. C. & G. PLAYFORD. 1985. Early Triassic megaspores from the Rewan Group, Bowen Basin, Queensland. Alcheringa 9: 297–323.

SEWARD, A. C. 1904. Catalogue of the Mesozoic plants in the British Museum—The Jurassic Flora, part 2, Liassic and Oolitic floras of England. British Museum (Natural History), London.

———. 1910. Fossil Plants 2. Cambridge Univ. Press, Cambridge.

———. 1913. A British fossil *Selaginella*. New Phytol. 12: 85–89.

——— & B. SAHNI. 1920. Indian Gondwana plants: a revision. India Geol. Surv. Mem. Paleontologia Indica 7: 1–54.

SINGH, C. 1964. Microflora of the Lower Cretaceous Mannville Group, east-central Alberta. Res. Council Alberta Bull. 15: 1–238.

———. 1971. Lower Cretaceous Microfloras of the Peace River Area, Northwestern Alberta. Res. Council Alberta Bull. 28: 1–299.

SKOG, J. E. 1986. The supposed fern *Onychiopsis psilotoides* from the English Wealden (Lower Cretaceous) reinterpreted as a lycopod. Canad. J. Bot. 64: 1453–1466.

———. 1990. *Wathenia*, the correct generic name for *Tanydorus* (Lycopodiales) sensu Skog, not as to type. Taxon 39: 306–307.

SNIGIREVSKAYA, N. S. 1980. *Takhtajanodoxa* Snig., a new link in evolution of lycopsids. Pp. 45–53 *in* S. G. Zhilin (editor), Systematika i Evolyutsiya Vysshikh Rasteniy. Leningrad. [In Russian.]

——— & I. N. SREBRODOLSKAYA. 1986. The first finding of petrified stems of *Pleuromeia* with preserved anatomical structure. Bot. Zhurn. Leningrad (St. Petersburg) 71: 411–415.

SREBRODOLSKAYA, I. N. 1988. Data on *Pleuromeia sternbergii* (Münster) Corda (Lycopodiophyta) from the Early Triassic of the Far East. Ezhegodnik Vsesoyuznoga Paleontologicheskogo Obshchestva 31: 179–195 [In Russian.]

SRIVASTAVA, B. P. 1946. Silicified plant-remains from the Rajmahal series of India. Proc. Natl. Acad. Sci. India, Sect. B., Biol. Sci. 15: 190–211.

SUKH-DEV. 1980. Evaluation of in situ spores and pollen grains from the Jurassic–Cretaceous fructifications. Proceedings 4th Internat. Palynol. Conf., Lucknow (1976–1977) 2: 753–768.

TAYLOR, W. C. & R. J. HICKEY. 1992. Habitat, evolution, and speciation in *Isoetes*. Ann. Missouri Bot. Gard. 79: 613–622.

TEIXEIRA, C. 1948. Flora Mesozóica Portuguesa. Serviços Geológicos de Portugal, Lisboa.

THOMAS, B. A. 1992. Paleozoic herbaceous lycopsids and the beginnings of extant *Lycopodium* sens. lat. and *Selaginella* sens. lat. Ann. Missouri Bot. Gard. 79: 623–631.

——— & D. L. MASARATI. 1982. Cuticular and epidermal studies in fossil and living lycophytes. Pp. 363–378 *in* D. F. Cutler, K. L. Alvin & C. E. Price (editors), The Plant Cuticle. Linnean Soc. Symp. Ser. No. 10. Academic Press, London.

TOWNROW, J. A. 1968. A fossil *Selaginella* from the Permian of New South Wales. J. Linn. Soc. 61: 13–23.

TRAVERSE, A. 1988. Paleopalynology. Unwin Hyman, Boston.

WALKOM, A. B. 1944. Fossil plants from Gingin. J. Roy. Soc. Western Australia 28: 202–203.

WANG, ZI-QUIANG & LI-XIN WANG. 1982. A new species of the lycopsid *Pleuromeia* from the Early Triassic of Shanxi, China and its ecology. Palaeontology 25: 215–225.

——— & YUN-YUN LOU. 1990. Studies on the megaspores of a mid-Triassic lycopsid in Shaanxi, China. Acta Bot. Sin. 32: 397–403.

WARD, L. F. 1905. Status of the Mesozoic floras of the United States. U.S. Geol. Surv. Monogr. 48: 553.

WATSON, J. 1969. A revision of the English Wealden flora, I Charales–Ginkgoales. Bull. British Museum (Natural History) Geol. 17: 209–254.

WHITE, M. E. 1981. *Cylomeia undulata* (Burges) gen. et comb. nov., a lycopod of the Early Triassic strata of New South Wales. Rec. Austral. Mus. 33: 723–734.

YAROSHENKO, O. P. 1975. Morphology of *Pleuromeia rossica* and *Densoisporites nejburgii* spores. Paleontological J. 9: 373–379.

ZEIGLER, A. M. 1990. Phytogeographic patterns and continental configurations during the Permian Period. *In:* W. S. McKerrow & C. R. Scotese (editors), Palaeozoic Palaeogeography and Biogeography. Geol. Soc. London Mem. No. 12: 363–379.

GENERIC CLASSIFICATION OF MODERN NORTH AMERICAN LYCOPODIACEAE[1]

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ABSTRACT

Generic classification of North American Lycopodiaceae is analyzed in terms of the general factors that govern the recognition of the rank of genus, the character states that determine affinities, the hypothetical common ancestral groundplan, a tree based on these data, and a translation of this information into a classification scheme. The genera segregated here are based primarily on numerous characters of anatomy, chromosomes, spores, and gametophytes. Those groups that are recognized as genera have many distinguishing features, strong gaps separating them from other groups, monophylesis, uniquely derived states, inability to hybridize, and a level of segregation consistent and comparable with generic division in other pteridophytes. The classification adopted is as follows: subfamily Huperzioideae (*Phlegmariurus*, *Huperzia*), subfamily Lycopodioideae (*Lycopodium*, *Diphasiastrum*), and subfamily Lycopodielloideae (*Pseudolycopodiella*, *Lycopodiella*, and *Palhinhaea*).

At the species level, the classification of North American clubmosses, all formerly placed in a single genus *Lycopodium*, has been altered radically since the eighth edition of *Gray's Manual* (Fernald, 1950). More rigorous definitions of species, and the inclusion of data from population biology, anatomical characters, cytogenetics, and interspecific hybridization, have been important factors in this change. Recently, a new question has arisen: What should be the classification at the generic level? The traditional classification has been challenged by such recent European workers as Pichi Sermolli (1977), Holub (1975, 1983), and Øllgaard (1987). The generic interpretation of Lycopodiaceae has also been influenced by researchers in North America including Beitel, Britton, Bruce, Hickey, F. Wagner, Whittier, and Wilce, who have contributed valuable new information on anatomy, spores, chromosomes, life cycles, habitats, and interspecific hybridization. In the following report we attempt to interpret this information.

We have asked the following questions: What criteria are used for recognition of genera in pteridophytes overall? What characters can be used to differentiate the groups of Lycopodiaceae in particular? What, if any, directionality can be deduced for each character trend? What were the character states of the probable ancestral source of modern Lycopodiaceae? How do the character changes fit into a tree of relationships? And how should this body of information be translated into an acceptable classification scheme?

For nearly 20 years pteridologists were under the impression that the different gametophytic types reported in Lycopodiaceae were merely results of environmental modifications, as proposed by Freeberg & Wetmore (1957). The gametophyte was therefore considered unreliable as an indicator of relationships. However, Bruce (1976b) and Whittier (1981) showed that this conclusion was based on experimental error. For the past decade and a half, the gametophytic differences between species groups of Lycopodiaceae have proved to be valuable taxonomic characters (Bruce, 1972, 1976a, b, 1979; Bruce & Beitel, 1979). Other characters such as spore sculpture (Wilce, 1972; Tryon & Lugardon, 1990) and chromosome numbers (see F. Wagner, 1992) became available only during the past several decades. Also, Bruce (1975) provided data on mucilage canals, and Øllgaard (1975, 1979) new insights into the structure of the sporangium wall. Altogether, we now have a substantial array of new comparative data to aid us in classification.

In North America there are nearly 50 recognized species. Remarkably, approximately two-fifths of these are nothospecies as opposed to orthospecies, i.e., taxa of reticulate origin as opposed to

those of normal divergent origin. For such a small clubmoss flora, there is, nevertheless, profound diversity, and as will be seen below seven discrete groups can be readily distinguished. The largest number of species in this family is in the tropics, where the family is made up largely of species related to *Phlegmariurus phlegmaria*. Only one of these is in North America, where it is found locally in southern Florida.

GENERIC DELIMITATION IN PTERIDOPHYTES

For generic delimitation there are far more gross morphological characters that can be used in angiosperms than in pteridophytes. Perhaps for this reason, workers familiar primarily with flowering plants have tended to lump Lycopodiaceae into one catch-all genus, simply because they all seem to look alike. However, when the plants are examined in detail, including many micromorphological characters, we rapidly become aware of multiple and often striking differences between pteridophyte groups. There are far more demonstrable differences between the groups of living Lycopodiaceae than between such filicean genera as *Dryopteris*, *Rumohra*, *Arachniodes*, *Polystichum*, and *Phanerophlebia* (Kramer & Green, 1990). If workers with Dryopteridaceae deal with the species groups of clubmosses and firmosses at the same level of generic discrimination, to maintain consistency they should accept seven genera of Lycopodiaceae in North America.

The reasons why taxonomists separate and recognize plant genera are numerous, and there is no widespread agreement on how to go about it. We have used the most dependable and objective criteria that we can adopt in delimiting the genera of Lycopodiaceae. They include the following: (a) The characters used for generic separation should be numerous, not only one or several. (b) It is imperative that there be strong gaps in the character patterns. There should be no intermediate taxa, whether these intermediates are produced by gradation in ordinary phylogenetic divergence or intermediates produced by interspecific hybridization. (c) No genus should be recognized if it can be shown that that genus arose from two or more sources, i.e., is polyphyletic whether by convergence or some form of reticulation. A genus should be monophyletic, with strong evidence for an immediate common ancestry of its species. (d) Lines should be based on uniquely derived character states. Parallelisms, convergences, and reversals can be used to bolster generic validity so long as their patterns and incidence show them clearly to

be separate, though similar, derived states. (e) More and more pteridologists regard the presence of "intergeneric" hybridization as evidence for not separating genera. If hybridization does occur between members of "different" genera, that is evidence for their taxonomic unity. In the case of Lycopodiaceae, there is no evidence of intergeneric hybridization, even though in some groups (e.g., *Diphasiastrum*, *Huperzia*, *Lycopodiella*) intrageneric hybridization is rampant. (f) Above all, good genera in one group of pteridophytes should be approximately equivalent to and comparable with genera in other groups. One family of pteridophytes should not be finely split and another be grossly lumped. The character states involved in generic separations in the Lycopodiaceae should be reasonably similar in number and kind to those used in other families of pteridophytes. For example, if we keep the following pairs separate, *Marattia* and *Angiopteris* (Marattiaceae), *Pellaea* and *Cheilanthes* (Adiantaceae), *Athyrium* and *Diplazium* (Dryopteridaceae), then, as will be mentioned below, we should certainly keep *Palhinhaea* separate from *Lycopodiella*, or *Diphasiastrum* from *Lycopodium*. There should be some consistency.

CHARACTERS USED FOR GENERIC PHYLOGENY AND CLASSIFICATION

In trying to develop a consistent taxonomy for Lycopodiaceae there are, of course, pitfalls. Dealing only with North American taxa could lead to erroneous conclusions because links in other parts of the world might be overlooked. However, we believe that the taxa elsewhere on the earth will either fit the generic system given here and can be easily accommodated within it, or new ones can be added to it (Holub, 1991; Øllgaard, 1987). Because of the gaps in the divergence patterns (Fig. 1), it is no problem to delimit the genera. Another potential pitfall in this, as in all, systematic syntheses, is incompleteness or lack of data. The fossil record, although perhaps rich in comparison with the majority of other plant orders, is still replete with vast lacunae. And the living record has not been completely examined, especially in the tropics and Southern Hemisphere. We recognize that future research may change our understandings and even our basic conclusions.

For determining character state polarities there is no single living genus or family that we can use for comparison outside of the Lycopodiaceae. The Lycopodiaceae as we know them are diverse modern survivors of an ancient lineage. We used for outgroup comparison mainly three of the well known